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**MICHIGAN ACADEMY OF SCIENCE
ARTS AND LETTERS**

VOLUME XXXV (1949)

PART I: BOTANY AND FORESTRY

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PART I: BOTANY AND FORESTRY

PART II: ZOOLOGY

PART III: GEOGRAPHY AND GEOLOGY

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ANTHROPOLOGY, LANGUAGE AND LITERATURE,

**MEDICAL SCIENCE, PHILOSOPHY, POLITICAL
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EDITORS

EUGENE S. McCARTNEY
FREDERICK K. SPARROW

VOLUME XXXV (1949)-

PART I: BOTANY AND FORESTRY

"Pusilla res mundus est nisi in illo
quod quaerat omnis mundus habeat."

— SENECA, *Naturales Quaestiones*

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BOTANY

A SEARCH FOR THE CORRECT COLCHICINE TREATMENT OF THE EMBRYOS OF *SCILLA* *SPP.* TO PRODUCE POLYPLOIDS*

WILLEM EDUARD DE MOL

INTRODUCTION

IN EXPERIMENTS with *Fragaria*, *Nicotiana*, *Petunia*, and *Rubus*, Derman (1938) proved the value of colchicine treatment of seed plants in which embryonic development takes place close to the surface of the ovary. Two years later De Mol (1940) described colchicine experiments with *Bellevallia*. The present paper deals with experimental methods adapted to various bulbous and tuberous plants to obtain clones with double the usual numbers of chromosomes.

Varieties of *Scilla sibirica* and *Scilla tubergeniana* were used in the experiments. These Scillae were chosen from among the bulbous plants because their exceptionally flexible flower stalks (especially *S. sibirica*) are well adapted to the method of treatment. Also, a bulb bears several stalks, each with a number of flowers. This habit provides a great many embryos per bulb. Although hyacinths have a large number of flowers, the stiffness of the stem and the arrangement of the flowers cause mechanical disadvantages in treatment. Tulips and daffodils mostly produce single flowers.

Four bulbs of *S. sibirica*, four of the triploid variety Spring Beauty (De Mol, 1942), and three of *S. tubergeniana* were potted at the end of October, 1945. Flowering started in an unheated greenhouse on the south side of the building on February 1. On February 10, after removal of the stamens, the first cross-pollinations were performed. Only the earliest flowers of two or three flower stalks were used; later ones were removed. Colchicine was applied 4, 9, 23, and 39 days after pollination.

* *Acknowledgment*: The author is indebted to the University of Amsterdam for laboratory facilities and to Dr. Teunis Vergeer, of Hope College, Holland, Michigan, for valuable assistance in the preparation of the manuscript.

Two methods of treatment were employed:

(1) A drop of the colchicine solution was placed on the ovary after the anthers had been completely removed. The surrounding petals were relied on to hold the solution in contact with the ovary. This method is satisfactory only while the petals remain turgid.

(2) The flower stalk having only the ovaries is bent into a small tube containing the colchicine solution and is held in place with a plug of cotton. This method prevents evaporation, and therefore little of the solution is lost. As controls, a number of flowers without stamens were allowed to develop naturally. Since experiments by other workers have proved that 2 per cent colchicine is effective, this amount was used in these experiments.

TABLE I
S. TUBERGENIANA ♀ × S. SIBIRICA ♂

Date of pollination	Date of treatment	Days between pollination and treatment	Treatment in hours	Method	No. of flowers	Ovary March 28	Ovary April 10	Yield May 15
Feb. 10	Feb. 14	4	6.5	Drop applied	1	Some swelling	Died off	None
Feb. 10	Feb. 16	6	24	Drop applied	1	Became yellow	Died off	None
Feb. 10	Feb. 18	8	9	Tube	1	Became yellow	Died off	None
Feb. 11	Feb. 15	4	48	Drop applied	1	Withered		None
Feb. 11	Feb. 17	6	7	Tube	2	Some swelling	Died off	None
Feb. 17	Feb. 23	6	6	Tube	3	No swelling	Died off	None
Feb. 18	Control	.	.		5	Normal swelling	Four died off	Three seeds

TABLE II
S. TUBERGENIANA ♀ × ♂ (SELF-POLLINATED)

Date of pollination	Date of treatment	Days between pollination and treatment	Treatment in hours	Method	No. of flowers	Ovary March 28	Ovary April 10	Yield May 15
Feb. 10	Feb. 14	4	4	Drop applied	1	Some swelling	Died off	None
Feb. 10	Feb. 16	6	6	Drop applied	1	Some swelling	Died off	None
Feb. 10	Feb. 18	8	8	Tube	2	Some swelling	Died off	One seed
Feb. 13	Feb. 19	6	6	Tube	1	Became yellow	Died off	None
Feb. 15	Feb. 19	39	14	Tube	3	Normal swelling	Normal swelling	Three seeds
Feb. 10	Control	1	Some swelling	Died off	None

The results of pilot experiments to determine the most favorable time lapse between pollination and treatment, the best length of exposure, and the most favorable crosses are given in Tables I-VI.

Tables I and II show that only very few seeds came to full development. This was true, however, of the controls and of the open-ground seed yield of these species. For example, in 1945 only 26 seeds were harvested from 16 deliverable bulbs. For the remaining experiments a species or a variety was used which, under normal circumstances, yields seeds abundantly. The temperature at which the crossings were performed was 3°-4° C., which was low.

The forming of the embryo under the influence of the solution probably took place only in the case of treatment after 8 days for 8 hours. Further breeding will determine this. The treatment for 14 hours 39 days after pollination is of very questionable value. Because of their low fertility these crosses were not repeated.

TABLE III

S. SIBIRICA ♀ × S. TUBERGENIANA ♂

Date of pollination	Date of treatment	Days between pollination and treatment	Treatment in hours	Method	No. of flowers	Ovary March 28	Ovary April 10	Yield May 15
Feb. 29	March 8	8	1	Tube	3	Normal swelling	Normal swelling	Seven seeds

TABLE IV

S. SIBIRICA ♀ × S. SIBIRICA VAR. SPRING BEAUTY ♂

Date of pollination	Date of treatment	Days between pollination and treatment	Treatment in hours	Method	No. of flowers	Ovary March 28	Ovary April 10	Yield May 15
Feb. 23	March 1	7	5	Tube	2	Normal swelling	Normal swelling	Seven seeds
March 5	March 9	4	4	Tube	3	Normal swelling	Normal swelling	One seed
Feb. 23	Control	3	Normal swelling	Normal swelling	Eight seeds

Since Tables III and IV show that *S. sibirica* sets seed more easily than *S. tubergeniana*, the experiments with it will be continued on a larger scale.

A period of four days between pollination and treatment is not too short for embryo formation. In the experiment, however, only one seed

resulted from three flowers. When seven days were allowed to elapse *between pollination and a treatment, seven seeds developed from two flowers.*

It would appear, then, that there are about five days between pollination and embryo formation in *S. sibirica*. New experiments are needed to answer this question.

It is interesting to note that pollen of Spring Beauty is fertile enough to produce considerable seed in spite of the fact that it is triploid (De Mol, 1942).

Table V shows that a cross between Spring Beauty and *S. tubergeniana* as the male parent is also sterile, even when ample time is allowed for the formation of the embryo (23 days).

TABLE V
S. SIBIRICA VAR. *SPRING BEAUTY* ♀ × *S. TUBERGENIANA* ♂

Date of pollination	Date of treatment	Days between pollination and treatment	Treatment in hours	Method	No of flowers	Ovary March 28	Ovary April 10	Yield May 15
Feb. 22	Feb. 29	7	2	Tube	2	Some swelling	Died off	None
March 2	March 25	23	5	Tube	2	Some swelling	Died off	None

TABLE VI
S. SIBIRICA VAR. *SPRING BEAUTY* ♀ × *S. SIBIRICA* ♂

Date of pollination	Date of treatment	Days between pollination and treatment	Treatment in hours	Method	No of flowers	Ovary March 28	Ovary April 10	Yield May 15
Feb. 22	March 2	9	2	Tube	1	Some swelling	Died off	None
March 8	March 12	4	1.5	Tube	2	Normal swelling	Died off	Three seeds
March 23	March 30	7	6	Tube	2	Normal swelling	Died off	Two seeds
March 28	April 4	7	6	Tube	2	Normal swelling	Died off	Three seeds
March 8	Control	2	Normal swelling	Died off	Eight seeds

Table VI shows that, in spite of colchicine treatment, seeds form fairly readily from *S. sibirica* var. Spring Beauty when crossed with the original species.

Treatment of 1.5 hours does not markedly interfere with embryonic development when only 4 days are allowed to pass between pollination

and treatment. Potentially, normal *S. sibirica* can produce 20 embryos from an ovary. Since few seeds were obtained, it is believed that they developed in spite of the colchicine treatment. They cannot at this time be sacrificed for microscopic examination, and only culture can determine whether polyploid embryos resulted from the treatment.

SUMMARY

Of the bulbous plants, *Scilla sibirica* was found to be best adapted for treatment by colchicine. Crosses of *S. tubergeniana* ♀ with *S. sibirica* ♂ proved almost sterile, as was the self-fertilized *S. tubergeniana*. Crosses of *S. sibirica* ♀ with *S. tubergeniana* ♂ were more productive. Crosses of *S. sibirica* ♀ by *S. sibirica* var. Spring Beauty ♂ yielded good seed, as did reciprocal crosses.

From the study of several crosses it appears that four days must elapse between pollination and treatment if any seed is to develop, but more seed results if an interval of seven days is allowed. Partial inhibition of seed formation is interpreted as an indication of the effect of colchicine.

The duration of exposure to 2 per cent colchicine extended from one to forty-eight hours. Treatment as short as one and one-half hours reduced the normal seed yield.

AMSTERDAM, THE NETHERLANDS

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TWENTY-FIVE YEARS OF TULIP IMPROVEMENT BY X-RAY*

WILLEM EDUARD DE MOL

INTRODUCTION

THE history of the European culture of tulips dates back nearly four centuries, when the first were imported from Turkey. In 1581 Matthias de Lobel described twenty-two varieties in his *Kruidtboeck* ("Book of Herbs"). The first mention of sowing tulip seed was made by Chrispyn van de Pas in 1636. In the seventeenth century Dutch "tulipmania" reached the point at which 11,500 guilders, or about \$4,600, was paid for a single bulb of a new variety. Double tulips were first recorded in 1665. Parrot tulips were known before 1800. The Darwin tulips that are popular at present were largely originated by hybridization; others arose by mutations and were recognized as such during the early part of this century, when the author first undertook the study of bulb culture. Early experiments with X-ray treatment of tulips produced the mutation Sparkling Pitt from the tulip William Pitt (Pl. I). Because it combined several improvements in one flower (see below) it markedly stimulated interest in this manner of producing mutations.

SPONTANEOUS MUTATIONS

Mutations in flower bulbs are no surprise to the grower or the experimenter. During a culture of many years spontaneous changes have been observed under field conditions. These mutated plants were isolated and multiplied vegetatively; they have preserved the mutated quality. Most of them have been propagated in great quantities as precious assets and, together with the mother varieties, have been marketed for many years; for example, Cordell Hull, Bonifacius, Merula, Monarch, Hudson, Hilde-

* *Acknowledgment*: The author is indebted to the laboratories of the University of Amsterdam and to Philips Ltd., Electric Works, Eindhoven, Netherlands, for the use of X-ray equipment and other facilities, and to Dr. Teunis Vergeer, of Hope College, Holland, Michigan, for valuable assistance in the preparation of the manuscript.

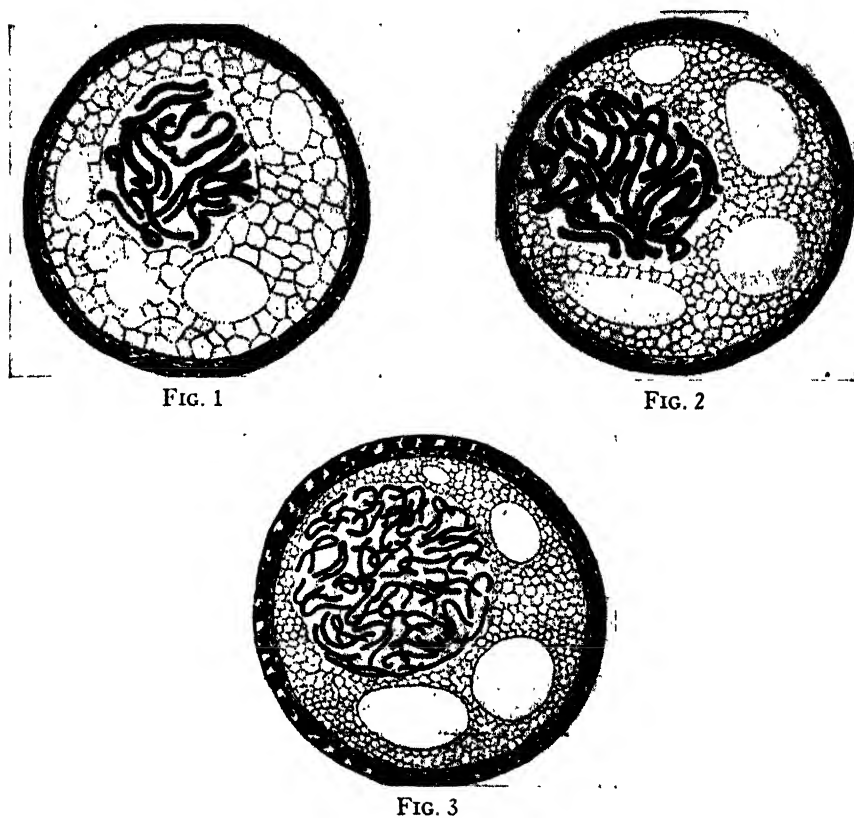
brand, Sedan, Tindal, and Unitas have been grown from the red Darwin tulip Bartigon. They represent as many somatic mutations in color from pink to red.

MUTATIONS DUE TO ALTERATION OF TEMPERATURE

That high- or low-temperature treatment during storage results in genetic changes was also established during the first quarter of this century (De Mol, 1929).

X-RAY MUTATIONS

Roentgen rays were first used in 1922. They appear to cause the same mutations as those which originate spontaneously in the field or by modi-



FIGS. 1-3. Haploid, diploid, and tetraploid pollen of tulips. Pollen grains progressively larger, but all figures are enlarged to same size. Photographs by J. Agterberg

fication of temperature, but they evoke the natural potentialities of tulips much more easily. The treatment is a valuable means of improvement for both the grower and the experimenter, but it cannot in one year produce bulbs with the desired characteristics. The mutation generally first appears as an aberration in color or shape in a single sharply defined sector of a normally colored petal. During the development of the plant in spring new small bulbs grow between the withering scales. They originate from the buds present at the time of planting in October of the preceding year. When these buds are in the mutated sector, the new bulbs retain this feature. One may note from year to year the gradual spread of the mutated characteristic, first to a perianth leaf, then to a sector of the plant, and finally to the whole plant (Pls. II-III).

Between 1928 and 1935 it was discovered that X-raying of hyacinths causes slow and feeble growth and that X-raying of tulips and hyacinths may result in doubling or quadrupling the number of pollen grains (Figs. 1-3). Microscopic studies showed that (1) the number of chromosomes varied owing to the arrest of nuclear division, (2) chromomeres separated from their chromosomes and often were stretched out into filaments, (3) chromosomes remained in the cytoplasm after nuclear reconstruction, (4) many pollen grains became sterile, and (5) somatic mutations also occurred (De Mol, 1933, 1937).

By 1940 the practical application of X-ray treatment had resulted in seventy-two distinct characteristics. The most notable among these represent modifications of the amount of anthocyanin, a blue, violet, or red pigment found dissolved in the cell sap. The variety Dido changed from orange pink to a lighter shade; Prosperity turned pink instead of white; Fantasy changed from pink to red; William Copland, from violet to pink; Roi d'Islande, from pink to violet. Yellow plastids formed in the dark-pink tulip Peach Blossom. Its mutation shows a mixture of red and yellow.

The color of the leaves is often modified; for example, Prince of Austria has a light-green edge, and Fantasy has developed a yellow stripe in the middle of the leaf, whereas green and yellow stripes alternate in Peach Blossom and Gemma (Pl. IV).

The shape of the flowers shows various aberrations after treatment; among them the edge of the perianth leaves is ragged in Van der Neer, the flower has become more globose in Roi d'Islande, the perianth leaves have sharper points in Clara Butt. The Parrot tulips are X-ray bud mutations whose perianth leaves have been enlarged from the normally formed General de Wet (Pl. V). The Parrots Gemma and Fantasy prove

that this process is not irreversible; by continued treatment they have been reduced to the normal flower shape. Fantasy and Red Champion have also developed different shapes and colors (Pl. VI, Fig. 1).

Several mutations may combine in a single new tulip. Sparkling Pitt is a sparkling dark-red bud mutation of the lighter-red William Pitt. The color is finer than that of the mother variety, and the flower, originally rounded off on the under side, has become somewhat squat, and a so-called butterfly heart¹ has developed at the base of the perianth leaves (Pl. I). It is an adornment to bulb culture, an asset to the trade, and an achievement of science.

In the hyacinths partial staminody, the partial metamorphosis of perianth leaves into stamens, has occurred. The three inner perianth leaves have become shorter and narrower. To the right and left the darker-colored tissue of the anthers is visible. At maturity this tissue bursts, and the yellow pollen appears. When microtome sections are made from these abnormally formed perianth leaves while they are young, one may clearly see the (sterile) pollen grains under the microscope.

The total number of mutations in hyacinths and tulips obtained after twenty-five years of X-ray treatment surpasses many times the number reported in publications.

Though even the smallest and least attractive deviations are important to science, only those varieties having a market value are raised on a large scale. Since 1940 a number of "X-ray tulips" without commercial value have been preserved by the author in a so-called Hortus Bulborum maintained for scientific research. Only one of the hyacinth mutations is still being propagated, since such culture is very expensive.

TEMPORARY MODIFICATIONS

In addition to permanent mutations, X-ray often results in modifications of a passing nature. During the first two years the X-rayed plants show, on the whole, a damaged aspect and an impaired growth (Pl. VI, Fig. 2). Though the amount of treatment has a definite influence on this phenomenon, such changes are bound to happen even with well-determined doses. The structure of the tulip bulb explains why plants appear to suffer most in the first two years after radiation. During the X-raying between July and November there exists in the bulb a large bud with a much smaller bud at its base. The first or final bud has progressed farthest and already contains the leaves and the flower for the next year.

¹ A yellow-white band above the blue spot at the base of the perianth leaves.

The smaller bud is a new starting point for the second year, with several small scales already split off. This bud also is reached by the X-rays and, when in the second year it grows into a plant, it still bears traces of the previous treatment. The buds which at the time of treatment had not developed show the mutated form, but develop more normally.

DIVISION HYPOTHESIS

The radiant day of April 24, 1937, will not easily be forgotten by the author. Dr. L. Randolph, of the Cornell University Agricultural Experimental Station, had asked permission to attend some experiments. In the laboratory he found a plant in full bloom; it was the tulip Prosperity, of which one half of the flower was dark red, whereas the other half was pure white.

To explain this result of X-ray treatment I proposed the division hypothesis (De Mol, 1942). The ordinary Prosperity has a pink flower. The process of division of the genes for pink had been hindered. When the mother nucleus divided into two daughter nuclei, these genes were kept in one daughter cell by the X-raying (duplication of genes) and consequently were not able to reach the other one (deletion). This daughter nucleus could not develop a pink anthocyanin; hence the white half of the flower. The first daughter nucleus, on the other hand, received all the genes for pink; hence the red half of the flower (cumulative effect). Many cases of bud mutation can be explained by duplication and deletion.

The origin of other modifications may be explained similarly. When the external conditions influence the cell in a uniform way, with the result that the division — albeit disturbed — proceeds equally, a modification lasting one or more years occurs. With an unequal influence and an inharmonious course of the division, cells with too many or too few chromosomes or chromosome fragments originate. This influence on the cytoplasm then causes the hereditary diversity.

SUGGESTIONS FOR X-RAY TECHNIQUE

The technique, experimentally developed since 1922, not only takes into account the doses, quality, and duration of the treatment, but also, and more especially, the phase and development rate of the bulb. This, of course, is closely related to the particular variety to be treated. During the first years tulips were exposed to various dosages of X-ray up to 1,000 roentgen units. After repeated experiments it was established that it was not wise to surpass 800 roentgen units.

The effects of the hardness of the rays showed plainest in Krelage's Triumph, in which the heaviest damage corresponded with the highest voltage. Full-grown large bulbs treated in August and September proved most satisfactory. They contain the greatest number of buds and young bulbs and, because of their dryness and hardness, are better protected against damage during transport and X-ray treatment.

If one wishes to bring out all the possible mutations and all the possible genetic changes in the bulbs that may result from one treatment, he should propagate them for at least four years.

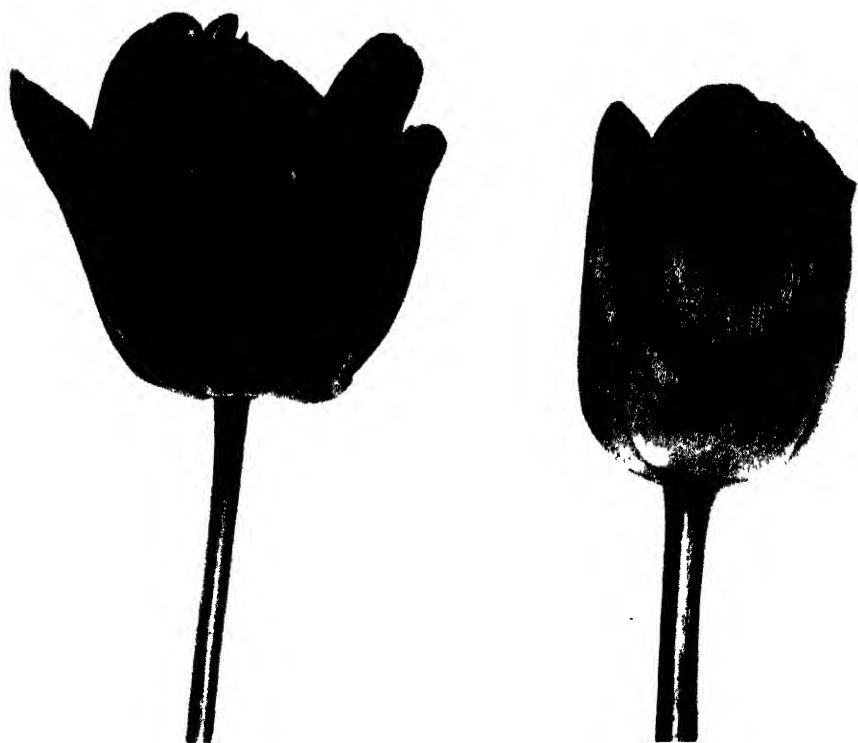
SUMMARY

The history of mutation in tulips is reviewed, and the results of X-ray treatment since 1922 are summarized. Concurrent nonhereditary aberrations are discussed. A "division hypothesis" based on duplication and deletion is reviewed. Treatment in August and September with dosages not in excess of 800 roentgen units are most successful.

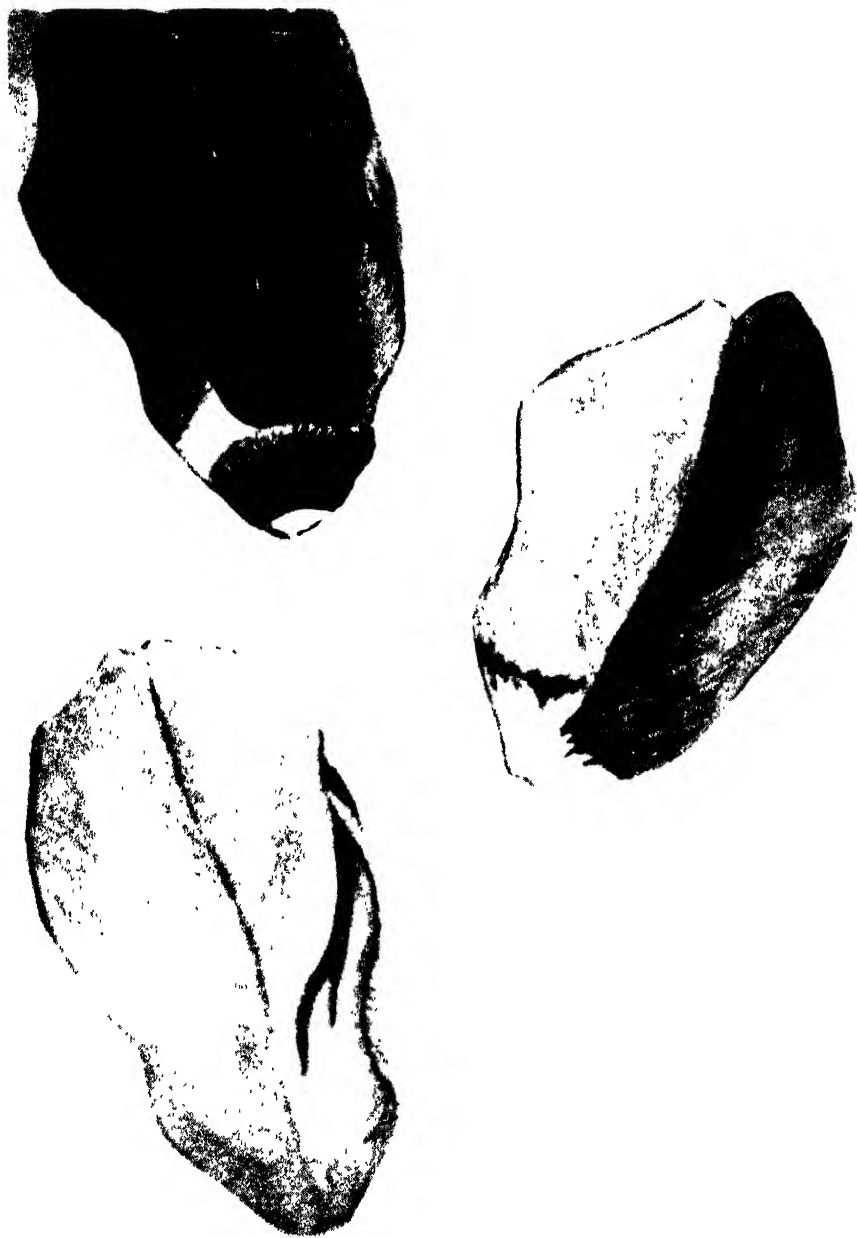
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Red Darwin Tulip William Pitt (right) and its X-ray mutation, Sparkling Pitt
(Photograph by J. Agterberg)



X-ray mutations in petals. Upper: Red, white and yellow sectors in a petal of Darwin Tulip Alland Pierson. Middle. Lighter sector in Darwin Tulip Bartigon. Lower: Small red sector in Mon Tresor. (From water colors by E. Loudon. Photograph by George Schneider)



FIG. 1



FIG. 2

White X-ray mutations in half of Parrot Tulip Red Champion (Fig. 1) and in half of Early Tulip Peach Blossom (Fig. 2). From water colors by E. Loudon. (Photographs by George Schneider)



Variegated leaf of Parrot Tulip Gemma
(Photograph by C. A van der Gen)

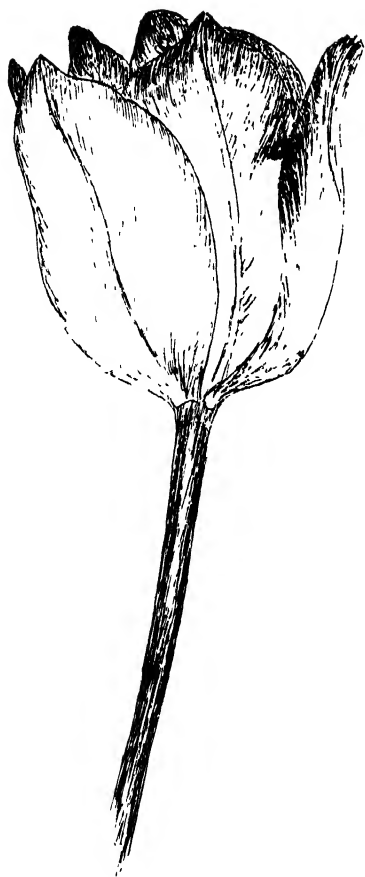


FIG. 1



FIG. 2

FIG. 1 Single Early Tulip General De Wet Drawing E. Loudon

FIG. 2 X-ray mutation form General De Wet to Parrot form



FIG. 1 Giant X-ray Tulip Red Champion
Photograph by J. Agterberg



FIG. 2. Aspect of damaged tulips the first year after X-ray treatment (Photograph by Agterberg)

THE EFFECT OF SIX VITAMINS UPON THE GROWTH OF *FUSARIUM SOLANI* IN A SYNTHETIC MEDIUM

SISTER MARY VIRGIL GHERING

THE culture of *Fusarium solani* used in this investigation was identified by Professor William C. Snyder,¹ of the University of California. It was carried on a potato-dextrose agar. Spore suspensions were made with a 5 per cent solution of peptone in normal saline, and were stored in a refrigerator. It had been reported to the author that such suspensions could be kept indefinitely under these conditions, but germination was observed after a few weeks, when spore counts were made with a hemocytometer.

Every component of the nutrient medium employed was chemically defined. A mixture of amino acids replaced the "vitamin-free" casein hydrolysate, which is used in many of the microbiological procedures for the assay of various vitamins. Hydrolysis of casein is usually effected by heating with strong acids, but it is doubtful whether the reaction is ever complete. The products of hydrolysis include, besides the alpha-amino acids, ammonia and humin. Tryptophane is lost in the insoluble humin fraction, while tyrosine is involved in the soluble brown humin. If hydrochloric acid is used, some cystine is destroyed in the subsequent removal of chloride ions by means of silver salts. Ordinary technical casein contains a considerable amount of vitamins. To remove completely traces of niacin and other vitamins, the casein is subjected to treatment with special activated carbons. The adsorption of amino acids and peptides by activated charcoal has been reported. It is probable, therefore, that casein hydrolysate varies from lot to lot according to the content of the original casein, the extent of hydrolysis, and the amount of treatment by norite for the removal of vitamins.

¹ Snyder and Hansen (1945) have proposed a revision of the taxonomy and nomenclature of the Fusaria. Their system is based upon evidence of variability, occurring in the progeny of cultures isolated from single spores of many so-called species in the genus.

Some microorganisms are able to synthesize all the amino acids they require from a single one or from asparagine. They display better growth, however, when a mixture of amino acids is furnished in equivalent amount in the culture medium. Robbins and Ma (1945) suggest that substances which are supplied in the medium may be incorporated into fungal proteins more rapidly than those which must be synthesized by interconversions in living tissue. Many fungi require a complex nitrogen source. The nitrogen requirements of these organisms are determined by omitting one component at a time from a mixture of amino acids which supports growth. When all the nonessential components are omitted at the same time, however, growth seldom results. Under these conditions additional amino acids are indispensable. Snell (1946) recommends the use of a complete assortment of amino acids for both vitamin and amino-acid assay.

The optimal combination of amino acids is not known. Since casein is the protein having most satisfactory nutritive properties, a synthetic casein hydrolysate has been widely used. However, it is not certain that casein supplies all the amino acids in ideal proportions. It is considered likely that the minimum protein requirement, as determined by the optimal combination of amino acids, may prove to be much lower than that secured with casein.

The amino-acid requirements of *Lactobacillus arabinosus* and *L. casei* were investigated by Hyma (1946). He used Snell and Wright's medium (1941) for the assay of niacin and Gladstone's medium (1937) as points of departure. Hyma tried more than five hundred combinations of amino acids, and as a result of his work formulated the amount of each one which gives maximum growth of the test organisms. This was the mixture used in the present investigation. It included the twenty commonly occurring amino acids plus the purine bases, adenine, guanine, and xanthine; the pyrimidine base, uracil; and asparagine. Asparagine has been reported to accelerate growth, especially in the earlier stages. The other substances have been shown to be accessory growth factors for the lactic-acid bacteria. Because of the fundamental unity which underlies all biochemistry, it is very likely that they act as growth-promoting substances for other organisms as well.

The stock mixture of amino acids was kept in a tightly stoppered brown bottle. As compared with casein hydrolysate, it is a very convenient nitrogen source. Casein hydrolysate contains no preservative; therefore the solution remaining in the bottle must be sterilized each time the stopper is removed. We did find it possible, however, to withdraw the

solution with a sterile hypodermic needle and thus eliminate the need for repeated sterilization.

A comparison of the relative values of asparagine, casein hydrolysate, peptone, and the amino-acid mixture is indicated in the tubes of Figure 1.

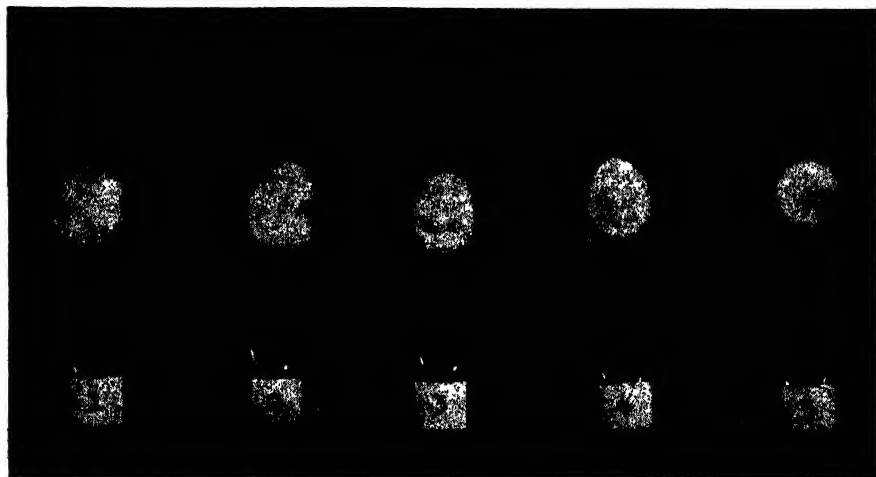


FIG. 1. A comparison of the effects of nitrogen from various sources upon the growth of *Fusarium solani* after six days on an agar medium containing sugar, salts, and asparagine. Tube 1 contained 8 mg. neopeptone; tube 2, 60 mg. casein hydrolysate; tube 3, 360 mg. casein hydrolysate; tube 4, 62 mg. amino-acid mixture. No addition was made to tube 5

Each tube contained eight milliliters of an agar medium made up of sugar, salts, and asparagine. To tube 1 was added peptone; to tube 2, casein hydrolysate in lesser concentration; to tube 3, casein hydrolysate in greater concentration; to tube 4, the amino-acid mixture. No addition was made to tube 5. The asparagine medium yielded a thin, spreading growth on the surface of the agar. The amino-acid mixture was not greatly inferior to the natural products when either extent or character of growth was considered. The edges of the colony, however, were more sharply defined. Casein hydrolysate in greater concentration gave less good growth than casein in lesser concentration. The latter produced the best growth if judged on the basis of diameter of colony, but peptone excelled in character of growth.

In this experiment it was observed that a deep-red pigment suffused throughout the peptone medium; but in the medium containing the amino-acid mixture not the slightest trace of pigment was produced. The asparagine medium acquired a pinkish-orange cast, and the casein-hy-

drolysate medium became pink. A deeper shade of color developed in the medium which contained the lesser concentration.

Subsequently the fungus was cultured on an agar medium with the amino-acid mixture as the nitrogen source and in the presence of single vitamins. Little difference was observed so far as colony diameters were concerned; but the presence of the vitamins, except p-aminobenzoic acid, seemed to encourage the spread of hyphae in the medium. No pigment was observed in any of the tubes except those which contained biotin and i-inositol. In the presence of these substances the medium became a deep-rosy red. It does not seem rash to suggest that the production of pigment in the media containing peptone and casein hydrolysate was due to the presence of vitamins in them. Many workers have reported the occurrence of various vitamins in peptone. After several weeks a faint-pink color was observed in all the tubes, except that containing p-aminobenzoic acid. If the production of pigment is evidence of the presence of biotin or i-inositol in the medium, their occurrence may be explained by the ability of the fungus to synthesize them at a very slow rate.

The initial pH of the medium seemed to have little effect upon the growth of the fungus. According to Wollenweber and Reinking (1935), this phenomenon is not unknown among the *Fusaria*. A potassium-citrate buffer was employed. The presence of the buffer in the medium resulted in a marked increase in growth, which seemed to be out of proportion to its effect upon the pH of the medium. It has been reported that beta-alanine is active only in the presence of biotin, thiamin, asparagine, and glutamic acid. Organic acids, however, and citric acid in particular, can replace the asparagine and glutamic acid. Citric acid reduces the optimal concentration of beta-alanine to a tenth of the usual amount.

The determination of the effect of a vitamin upon the growth of the fungus was practically the same procedure that is employed in microbiological assays of vitamins. A basal medium was prepared containing all the vitamins except the one under test. The sugar, salts, and amino acids were dissolved in distilled water over a steam bath. Appropriate amounts of the trace salts, buffer, and vitamin solutions were added, and the volume was brought to one liter. The solution was divided into ten portions, and the vitamin under test added in amounts calculated to give the desired concentrations. Biotin and folic acid were added after sterilization. The stock solutions of these vitamins were made up with sterile distilled water, and were stored in a refrigerator.

The volume of nutrient solution employed for culturing the test organism was 25 milliliters in 125-milliliter Erlenmeyer flasks. A standard

loop was used for inoculation. One loopful of the spore suspension was the standard inoculum for both the liquid cultures and the agar slants. The cultures were agitated after inoculation, but were incubated without agitation for six days at 27° C. Growth was determined by autoclaving the cultures, filtering, and drying the mycelial mats to constant weight at 100° C. The filter papers had previously been numbered, folded, and dried on watch glasses to constant weight. They were stored in a desiccator.

No vitamin proved to be essential for growth of *Fusarium solani*. Biotin, folic acid, and calcium pantothenate, however, stimulated growth. When the average dry weight of mycelium in milligrams was plotted against the concentration of these vitamins in gamma per milliliter, S-curves were obtained. The stimulatory effect of these vitamins may be due to the inability of the fungus to synthesize them as rapidly as they can be used if furnished from the outset in the culture medium.

It is not surprising that biotin should exert a beneficial effect upon growth. Barnett and Lilly (1947) secured some evidence that the ratio of the weight of biotin in the medium to the weight of mycelium at the time of perithecial formation must be at least one part to twenty million for perithecial formation to occur. Folic acid may be synthesized by microorganisms in the digestive tract. Persons getting sulfa-drug treatment occasionally develop a white blood cell deficiency. The same type of blood disorder appears in persons who have been deprived of folic acid. Elvehjem (1943) suggests that the sulfa drugs may destroy the microorganisms in the intestinal tract which ordinarily manufacture folic acid. In view of the almost universal occurrence of pantothenic acid in tissue extracts, the slightly beneficial effect of calcium pantothenate is not difficult to understand.

These experiments indicate that pyridoxine and riboflavin are without effect upon the growth of *Fusarium solani*. Pyridoxine was discovered in studies of animal nutrition, and with the exception of a few species of *Ceratostomella*, fungi do not require it. Hawker (1944) stated that riboflavin, niacin, and the fat-soluble vitamins had not so far been reported essential for the growth of any fungus, although some species were known to synthesize one or more of them. It may be that they play a rôle in the biosynthetic processes of fungi, but that all fungi are able to synthesize them.

Niacin seemed to exert an injurious effect upon growth, which was greater in the absence of niacin than under any other condition of the experiment. This might be due, however, to changes in the composition

of the medium during heat sterilization. Knight (1945) affirms that heating asparagine and glutamic acid together in the presence of manganese and air yields nicotinamide, which was identified by isolation and characterization. Since these substances were present in the medium, it may be that the harmful effect of niacin was due to its presence in excess.

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SOME NUTRITIONAL ASPECTS OF THE PISTILLATE CONDITION IN RAGWEEDS *

KENNETH LESTER JONES

THE giant ragweed, *Ambrosia trifida* L., is monoecious with pistillate flowers in the leaf axils and staminate flowers in conspicuous racemes. I have not seen deviations from this pattern in nature.

In 1945 I collected in one locality along the Huron River near Ann Arbor, Michigan, seed infested with larvae. The following spring sixty-four plants were grown from them, eight of which bore some pistils in the racemes. The leaves were misshapen and blotched with yellow areas.

I was then carrying on photoperiod experiments and found, as had Mann (1942), that plants of *A. trifida* given six hours of light a day produce pistillate structures in place of staminate. The seed that occasionally form from such abnormally developed pistils are about one third the usual size. It happened that the first that I succeeded in germinating grew into dwarfed plants with misshapen leaves (Pl. I, Fig. 1) and pistillate racemes.

These observations suggested that sex reversal may be brought about by a deficiency of food in the cotyledons. A simple experiment was therefore run to test the effect of the removal of cotyledons from normal seedlings. Carefully selected seed were sown on June 11, 1947, and the plants were grown in the greenhouse under normal light conditions of the summer season. The results are given in Table I.

The occurrence of a few aberrant plants in the control was hardly expected, since I had encountered none either in nature or under ordinary conditions of cultivation. No significant increase in sex reversal was brought about by the removal of cotyledons or plumule. (Plate I, Figure 2, shows some of the altered racemes.) I had previously reported (1936) that in Form 2 of *Ambrosia elatior* excision of the plumules increased the pistillate plants by 6.4 per cent.

In the meantime additional information has been obtained on the

* Paper from the Botanical Gardens and the Department of Botany, University of Michigan, No. 894.

offspring from seed of sexually reversed plants from the photoperiod work. Such minute seed do not, as first supposed, ordinarily form individuals with pistillate racemes. To date (April, 1949), 230 plants have been grown and only 7 have borne racemes with pistillate flowers. Dwarfing is likewise not the rule, since only 6 plants showed this condition, 3 being pistillate.

Pruning and defoliating of plants in which floral primordia have formed appreciably increases the percentage of sex reversals (Table I).

TABLE I
THE FORMATION OF RACEMES WITH PISTILLATE HEADS
IN AMBROSIA TRIFIDA

Material	No. of plants	With racemes	Racemes pistillate	Percentage pistillate
Control	100	96	1	1
Cotyledons removed .	100	91	3	3
Plumule and cotyledon removed	102	85	2	2
Pruned	50	46	6	12
Defoliated	109	48	14	12
Defoliated, sucrose ...	71	24	5	7

The pruned plants were cut back to bear only one leafy branch. The plants that were defoliated were grown as individuals with two equal, opposite branches; one branch was left intact, and the other was completely defoliated when floral primordia appeared. As Table I indicates, over 50 per cent of the defoliated branches failed to produce racemes. The foliated branch always gave rise to staminate racemes.

A second set of defoliated plants was sprayed with a 10 per cent aqueous solution of sucrose in which "carbowax" was used as a spreader and sulphanilamide added to keep down the growth of fungi. The percentage of reversals to the pistillate condition was slightly less than that of the corresponding set not receiving sucrose, but there was a considerable increase in racemeless individuals.

Tampering with the nutrition of Ambrosia plants in the early vegetative stage seldom leads to a sex reversal. This is borne out by the present work and by previous reports of negative results when mineral nutrients were added to the soil (Jones, 1936) and when plants from ten to twenty days old were exposed to short days (Jones, 1947).

Once floral primordia are initiated, several external agents of unlike

nature bring about an alteration from staminate to pistillate structures. Short-day treatment is particularly effective, but defoliation and the application of chemicals to the stem apex may give results. I have had some positive results by using indole acetic, phenylacetic, and α estradiol propionate (Pl. II, Figs. 1-2). The change from the pistillate condition of the lateral flowers to the staminate is rare, but two instances were noted (Jones, 1947).

The fact that defoliation alone is sufficient to produce sex reversal is a vexation to the experimenter studying the effects of photoperiodism. If he takes a two-branched foliated plant and gives one branch short-day exposures, the treated branch will usually form some pistils in its raceme, whereas the branch receiving the normal photoperiod of late summer will be staminate. If the untreated branch is defoliated, it will very likely become pistillate, but it is impossible to ascertain whether this reversal in a given specimen is the result of defoliation or of a transfer of some stimulus from the short-day branch.

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PLATES I—II



FIG. 1. Malformed leaves of *A. trifida* pistillate plants. The parent plants underwent sex reversal from short-day treatments



FIG. 2. Pistillate racemes of *A. trifida* from plants from which the cotyledons had been removed



FIG. 1. Branch of *A. elatior* bearing staminate racemes (control)



FIG. 2. Branch of *A. elatior* on the same plant and opposite to the one shown in Figure 1. This cluster of four racemes, three of which show some pistillate structures, developed from a stem apex to which α estradiol propionate had been applied

SOME ECOLOGICAL ASPECTS OF THE ACRASIALES IN AND NEAR MADISON, WISCONSIN

EUGENE D. KITZKE

INTRODUCTION

IN THE Myxomycetes there is a relatively small group known as Acrasiales. They are strikingly different from true Myxomycetes in that the individual myxamoebae retain their plasma membranes, keep their individuality, and form a pseudoplasmodial stage. The plasmodial stage of the true Myxomycete differs, of course, in that it has no individual cells and is a naked mass of multinucleated cytoplasm.

Since the group as now known is a small one, a concise study of its distribution in a limited area can be made in a summer's work. Sixty soil samples from various localities within a twenty-five mile radius of Madison were tested. In addition, an attempt was made to find significant correlations between certain measurable factors of the soil and the presence of the organisms. The soil factors of pH, the percentage of organic matter, and the colloid percentage were determined for each sample. The plant associations of each soil source were also considered as variable factors.

MATERIALS AND METHODS

Of sixty soil samples thirty-six yielded members of the Acrasiales. From these, four species were identified. Two belonged to the genus *Dictyostelium* and two to *Polysphondylium*.

Representative field samples of grassland, marshland, sand dunes, shrub areas, and humus from various stands of hardwood forests were collected in sterile 60 c.c. bottles. They were taken to the laboratory, where they were processed almost immediately by various soil-analysis procedures (to be described later).

METHOD OF ISOLATION

The soil sample was poured out on a fresh paper towel, and particles or crumbs of it selected at random were placed on petri dishes of soil

agar (Singh, 1946). Ten plates were prepared from each sample in order to permit a calculation of the distribution frequency percentage for the organisms. Incubation was carried out at room temperature (summer temperatures ranging from 22° to 26° Centigrade) for four days, after which the plates were examined for fruiting structures of the fungus.

Plates containing the fruiting structures of the Acrasiales were set aside an extra day for further development to permit heavier growth. The next day the remaining plates, hitherto blank, were reexamined to determine whether any slower-growing forms had appeared, a thing that rarely happens. Plates bearing the desired organisms were then transferred by inoculation of terminal sorus spores to petri plates of mannite agar (*Difco Manual*, 1937) already supporting a streak growth of *Escherichia coli*.

The bacterial population of the streak afforded abundant food for the Acrasiales, and they attained luxuriant growth in this mixed culture. Often the transfer from soil agar carried along with it contaminants, the growth of which was eliminated by a second transfer. The organism, when finally isolated into a "pure-mixed"¹ culture (Raper, 1937), was transferred to a mannite agar slant for stock culturing and identification. Since the Acrasiales require bacteria for food, they must be kept in such a culture.

Because soil is a rich source of a great variety of fungi, the medium originally used to isolate the Acrasiales had to be one that could limit the number of contaminants. Experience with mannite agar has shown that heavy growth of unwanted forms of fungi occur on the plates and may obscure the more delicate Acrasiales. This could be obviated if precautions were taken to incubate the plates at 15° to 16° Centigrade for a two-week period; but this technique was impracticable in the present study because of summer temperatures and lack of incubator space.

The use of soil agar as the initial isolating medium greatly expedited matters, for Acrasiales, if present, appeared after four days' incubation at room temperature. The low nutrient value in this medium prevented the normal overgrowth that occurred in the comparatively rich mannite agar. The soil-extract agar was prepared after Hesseltine (paper in preparation). Its composition was as follows:

¹ The term "pure-mixed" as applied to a culture refers to the growth of some suitable bacterium and a member of the Acrasiales, each in pure culture, in the same dish or tube.

Agar agar	15 gm.
K ₂ HPO ₄	0.5 gm.
Glucose	1 gm.
Soil extract ² ...	100 c.c.
Tap water	900 c.c.

The original purpose for which this medium was designed was to isolate and culture mucors without getting a heavy overgrowth of contaminants or of the mucors themselves. Hesseltine noticed that it also lent itself rather consistently to supporting the growth of members of the Acrasiales. Thus it was adopted by the writer.

TECHNIQUE OF SOIL ANALYSIS

The soil samples were processed immediately after collection. The pH was determined by means of a Beckman pH meter. The approximate percentages of organic matter in them were ascertained by the use of the ash technique of Schollenberger (1931). When the margin of error due to carbonates and other compounds that may have been oxidized has been taken into consideration, the values obtained may be considered approximations.

The colloidal percentage was determined for each sample by the use of the Cenco-Wilde³ test, known as the hydrometer field test.

ORGANISMS ISOLATED

Four species belonging to two genera were isolated. Two, *Dictyostelium mucoroides* and *Polysphondylium violaceum*, occurred very commonly. In a small number of plates *Polysphondylium pallidum* appeared, a not uncommon species, according to Raper (1940), and *Dictyostelium minutum*, which is perhaps rare, since it has been reported infrequently in the literature.

Polysphondylium violaceum

P. violaceum has been described in an earlier paper by Kitzke (1950).

Dictyostelium mucoroides Brefeld

The measurements of the spores of *D. mucoroides* Brefeld, 3–5 × 5–8 μ, are somewhat larger than those given by Olive (1902); he does

² The soil extract was prepared by heating one kilogram of soil with one liter of tap water in an Arnold sterilizer for one hour, after which it was filtered two or more times until clear and then autoclaved for one hour on two successive days.

³ Cenco-Wilde Soil Colloid Tester No. 28250.

state, however, that the range is great. The diameters of the sori range from 100 to 600 μ , which agrees with Olive's measurements. The heights of the sorocarp differ greatly, ranging in many from 5 mm. in some to well over 1 cm.

Dictyostelium minutum Raper

The spores of *D. minutum* measured $3-3.5 \times 5-7 \mu$. An extensive study of their sizes revealed none outside this range, which is identical with that given by Raper (1941). The heights of the sorocarp ranged from 350 to 750 μ . The sori exceeded very little the largest diameter in the range (75 to 150 μ) listed by Raper. In spite of the ample food supply and the frequent transfers the growth of the organism was consistently small, which indicates that the species is different from any described, except *minutum*.

Polysphondylium pallidum

P. pallidum, described by Raper (1940) as of common occurrence, was found only infrequently in our samples. The measurements of the isolate, which correspond closely with those listed by Olive, are as follows: spores, $3.5-4 \times 7-8 \mu$; terminal sori, 50-90 μ in diameter; lateral sori, 30-40 μ in diameter; sorocarp, 300-400 μ tall.

CORRELATIONS

The sites of collection, all within a twenty-five-mile radius of Madison, are listed in Table I.

TABLE I
SOURCES OF THE SOIL SAMPLES

<i>Site</i>	<i>Location</i>
Grady tract	University Arboretum
Stewart's woods	Dane County
Bascom woods	University campus
Wollein's woods	Jefferson county
Willow drive	University campus
Grasslands	Forest Products Laboratory Road
Pine barrens	Arena
Prairie	Lake Mills

The pH values of the soils tested were within a narrow range and afforded little variation to enable me to detect growth patterns. When,

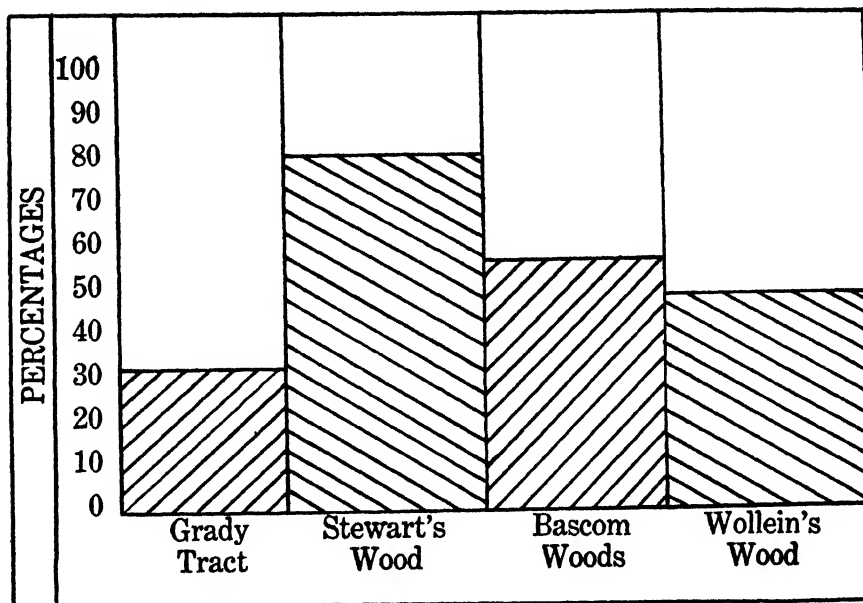


FIG. 1. Frequency percentage of *Acrasiales* in four quadrats

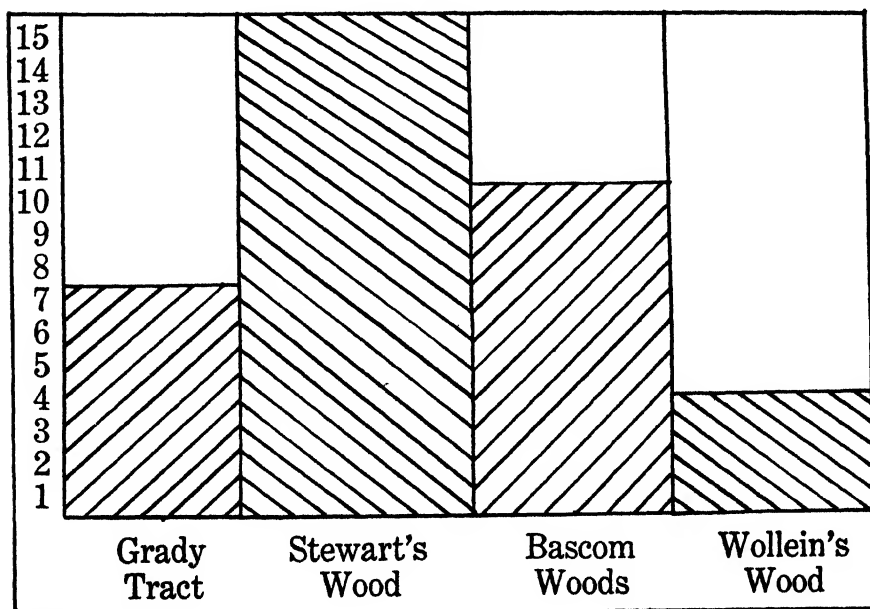


FIG. 2. Number of shrub species

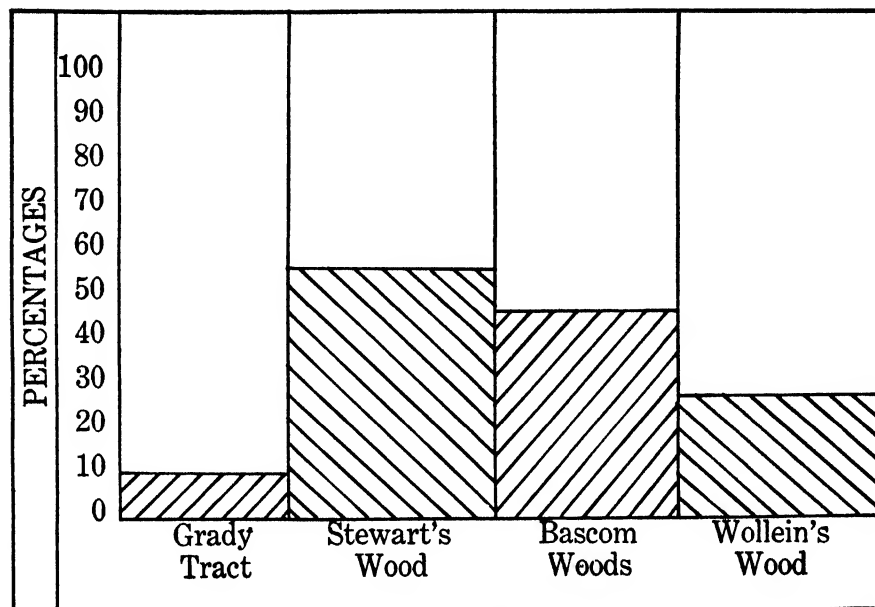


FIG. 3. Frequency percentages of herb species in four oak quadrats

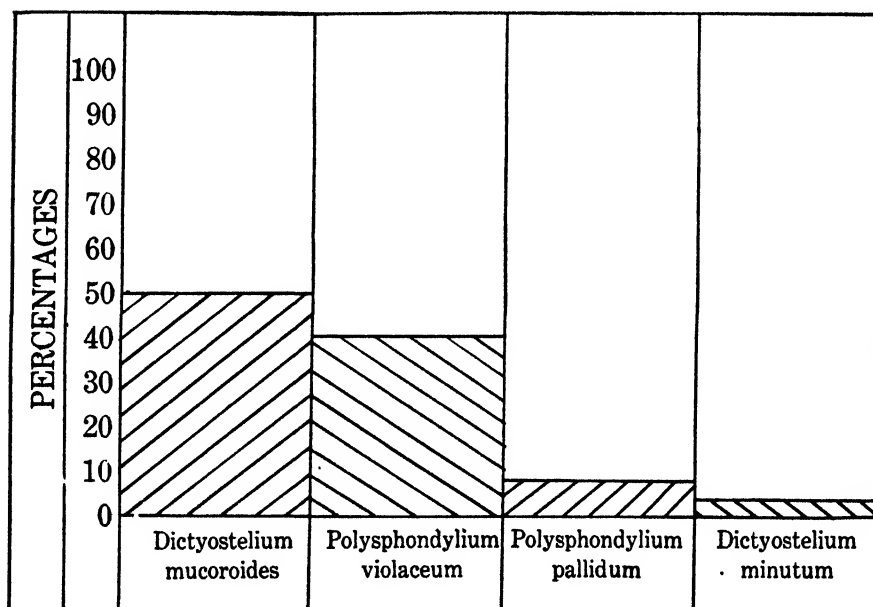


FIG. 4. Relative percentages of Acrasiales isolated

however, a large number of pH values below 6 were found, which, according to Raper (1939), is definitely not optimum, there was less growth of Acrasiales.

Soil colloid percentages and minimum organic percentages do not seem to have any obvious correlation with the presence of the organisms. In general, however, with the increase in the percentage of organic matter there is an increase in the frequency percentage of Acrasiales.

Figure 1 shows the frequency percentages of Acrasiales in the four quadrats which were studied thoroughly from an ecological viewpoint. Stewart's woods has the highest frequency percentage of Acrasiales and also the heaviest occurrence of herbs and shrubs. In fact, the graphs showing the data for the herb and shrub species (Figs. 2-3) closely resemble those for the occurrence of Acrasiales in these quadrats. This may be due to the greater number of bacteria decomposing the herb and shrub litter, which accumulates more rapidly in Stewart's woods than in Bascom woods, the Grady tract, or Wollein's woods. Thus an increase in the number of bacteria provides a greater food supply for the Acrasiales, and hence enables them to attain more uniform distribution.

Of the sixty samples taken and tested 60 per cent contained members of the Acrasiales. Only 40 per cent showed a complete absence of them or failure of the organisms to develop from them when inoculated with soil. The percentages of the different species found in the successful plates are given in Figure 4.

The total number of isolations was 157, composed of the following species: *Dictyostelium mucoroides*, 76; *Polysphondylium violaceum*, 60; *P. pallidum*, 12; and *D. minutum*, 9. These figures seem to be indicative of their relative distribution in the soils tested and confirm in general the reports of other workers (Raper, 1940; Olive, 1902).

SUMMARY

Members of the Acrasiales were isolated from soil samples taken at random within a twenty-five-mile radius of Madison, Wisconsin. The experiments show that soil agar provides an excellent isolating medium and that mannite agar used in connection with "pure-mixed" cultures is a good medium for stock culturing. The Acrasiales occurred in 60 per cent of the sixty soil samples tested.

No correlations for colloidal percentages were noted. With respect to the percentage of organic matter of the soil samples there was found to

be an increase of Acrasiales, with an increase of organic material in the soil.

The factor of pH does not seem to affect the frequency of occurrence of Acrasiales, mainly because of great variability in soil types. There seems to be a lower frequency percentage of Acrasiales, however, in plates inoculated from soils near pH 5 and 8.

Four species of Acrasiales were isolated representing two genera. Three species, *D. mucoroides*, *P. violaceum*, and *P. pallidum*, were reported common by other workers. One, *D. minutum*, first isolated by Raper (1941), appears to be relatively rare. *P. pallidum* also occurs only infrequently in this study.

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THE EFFECT OF HORMONE ON BARK RE- NEWAL IN *HEVEA BRASILIENSIS**

THOMAS J. MUZIK

BARK renewal of *Hevea brasiliensis* Muell. Arg., the Pará rubber tree, after tapping has been the subject of considerable investigation. It has been reported that various substances increase the rate of renewal. Beeley and Baptist (2) found that palm oil improved it from 25 to 50 per cent over a three-month period, although, strangely enough, Baptist (1) obtained no increase one year after applying indolyl-acetic acid, and he ascribed this lack of effect to the weak concentrations used, 1:1,000, 1:5,000, and 1:10,000 in lanolin. Other workers have reported that a number of substances are more or less effective, namely, mineral oil (2), coal tar (9), cow dung and clay mixture (1), tar (10), a solution of MgCl and NaCl in water, and distilled water alone (6). Sharp (8) noted that healing of large stumps was promoted by treatment with cow dung and Hessian cloth, whereas linseed oil and zinc oxide had no effect, and an asphalt-kerosene mixture retarded healing. Gandrup (4) claimed that tar had no effect on bark renewal.

Since many of these substances probably contain hormones and since the results reported above conflict, the author undertook the experiments here described.

MATERIALS AND METHODS

These experiments were carried out on the Firestone Plantations in Liberia, West Africa, from December, 1945, to March, 1946, the "dry season" in that part of the tropics. The clone Avros 152 was chosen because the bark is reasonably free from knots or ridges, and natural renewal is relatively slow. Only the lower half of each panel was treated; the upper half served as the control (Pl. I). Thus each tree was used for

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This work was done while the author was a member of the Research Department of the Firestone Plantations Company, Harbel, Liberia. It is published with the permission of the Company.

both treatment and control, and the relative growth rates of treated and untreated zones of the same panel could be measured. This method eliminated variation due to different growth rates of trees, a factor which may well have influenced the results reported above. As La Rue (7) has pointed out, the rate of renewal is affected greatly by many environmental conditions, such as soil and the tapping system, as well as hereditary factors.

Two hormones were tested, both in lanolin, indole-3-acetic acid in concentrations of 1:1,000, 1:5,000, and 1:10,000, and indole-butyric acid in concentrations of 1:1,000, 1:5,000, and 1:10,000. The effect of pure lanolin was also tested. Five trees were treated with each concentration of hormone daily, immediately after tapping. The hormones were applied in the same manner as panel fungicides, that is, with a small brush and directly on the bark tapped on the same day. Bark thickness was measured at monthly intervals, by means of a standard bark gauge. An average of three measurements was taken at each reading, although the variation in thickness was considerably less in this clone than that reported by Haigh (5) for certain seedling trees.

These trees were planted as seedling stumps in 1928 and grafted in 1933, when four to five years old. They were first tapped in 1939 on a half-spiral system, then placed on a full spiral from July, 1942, to March, 1943, and returned to the half spiral in March, 1943. The panel was about twenty inches from the graft union, and the average girth at sixty-five inches above the union was 61.7 cm. The tapping cut was at an angle of 30° from left to right and was made from the upper side down toward the cup (Pl. I). An especially good worker was assigned to these trees to insure even tapping. The bark was removed to a depth of one millimeter from the cambium. The trees were tapped on alternate days, and one fifteenth of an inch¹ of bark was excised at each operation. Frequent inspections of the trees were made.

EXPERIMENTS WITH INDOLE-3-ACETIC ACID

Indole-3-acetic acid was used in the first treatments. It was applied daily in concentrations of 1:1,000, 1:5,000, and 1:10,000 in lanolin. Bark thickness was measured at monthly intervals for three months after treatment. The initial thickness was one millimeter. The depth of renewed bark after treatment is shown in Table I.

¹ Note the two systems of measuring; the depth of tapping is invariably measured in the metric system and the amount of bark removed, in the English system.

TABLE I

THE EFFECT OF INDOLE-3-ACETIC ACID ON BARK RENEWAL

In all these experiments the lower half of the panel was treated and the upper half served as a control.

Tree	Bark thickness in millimeters		
	First month	Second month	Third month
LINE A. Concentration 1 : 1,000			
1 Treated	7.2	7.8	7.8
Control	6.7	6.8	7.0
2 Treated	8.3	9.2	9.3
Control	6.2	6.3	7.2
3 Treated	8.3	9.6	11.0
Control	5.7	6.9	8.5
4 Treated	8.7	9.9	10.5
Control	6.5	7.0	7.8
5 Wind-damaged
Average:			
Treated	8.13	9.13	9.65
Control	6.28	6.75	7.63
Difference	1.85	2.38	2.02
Increase	29.5%	35.3%	26.5%
LINE B. Concentration 1 : 5,000			
1 Treated	7.5	9.5	9.6
Control	7.7	7.8	8.0
2 Treated	8.1	9.1	9.2
Control	4.8	6.0	6.4
3 Treated	9.5	10.8	10.8
Control	6.1	8.5	8.7
4 Treated	7.3	7.4	9.0
Control	5.5	5.9	6.2
5 Treated	6.1	7.1	7.3
Control	6.1	6.5	7.2
Average:			
Treated	7.70	8.78	9.18
Control	6.04	6.94	7.30
Difference	1.66	1.84	1.88
Increase	27.5%	26.5%	25.8%
LINE C. Concentration 1 : 10,000			
1 Treated	7.2	10.0	10.3
Control	6.0	7.7	8.0
2 Treated	6.9	7.0	7.5
Control	5.1	6.1	6.3
3 Treated	7.7	9.0	9.2
Control	6.7	7.1	7.5
4 Treated	8.0	8.1	8.6
Control	5.7	6.2	6.8
5 Treated	6.9	8.0	8.6
Control	5.0	5.2	5.4
Average:			
Treated	7.34	8.42	8.84
Control	5.70	6.46	6.80
Difference	1.64	1.96	2.04
Increase	28.8%	30.3%	30.0%

These experiments were not continued for more than three months because abundant production of stone cells in the bark made accurate measurements very difficult. Later measurements indicate, however, that the treated portion of the panel maintains its greater thickness for at least five months after treatment.

The increase in bark thickness due to the hormone application was

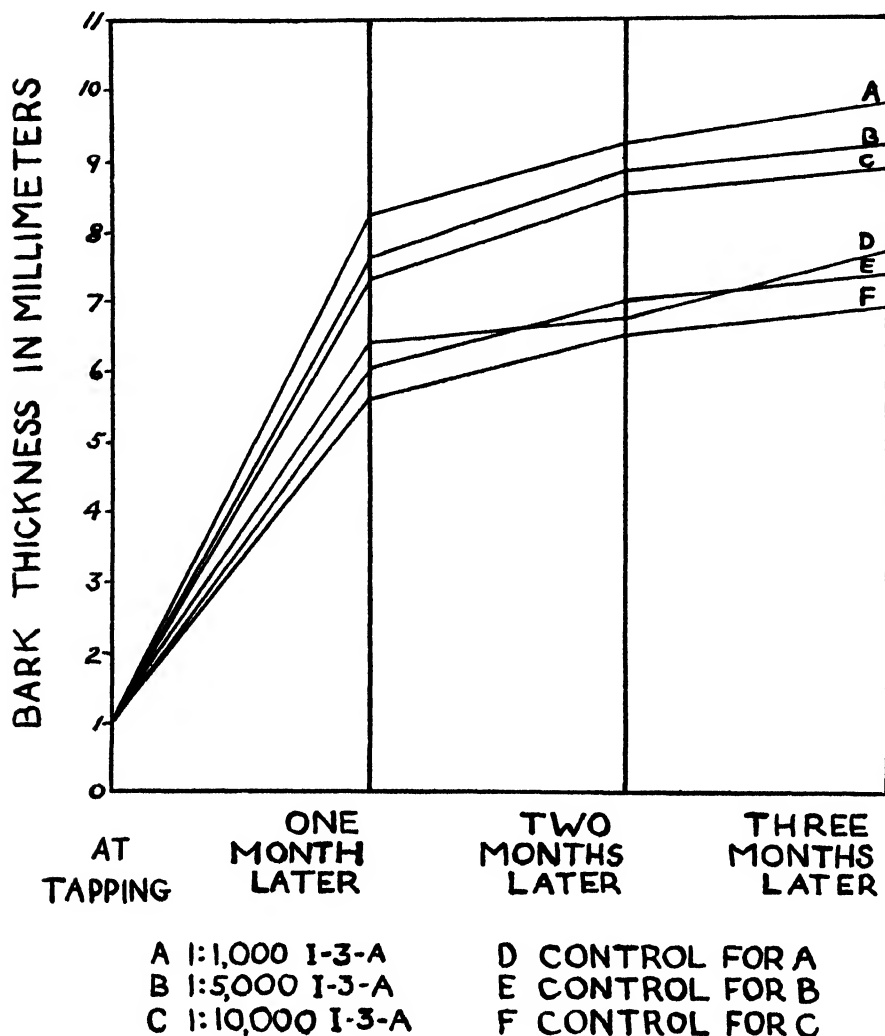


FIG. 1. Bark renewal in Avros 152 over a three-month period. A separate control is measured for each treatment (see text)

clearly visible as a swelling on the treated zone of the panel. A striking feature of this experiment was the greater quantity of latex exuding from the treated zone than from the untreated zone, possibly indicating a better developed latex system. As Bobilioff (3) has shown, formation of new latex vessels takes place very soon in renewing bark. However, definite proof that more vessels are formed in the treated zone must await histological examination.

The most rapid renewal of bark occurs in the first month after tapping; it tapers off in the second and third months. Figure 1 shows the relative rates of renewal over the three-month period. The 1:1,000 concentration exhibited the greatest effect, giving an increase over the control of 29.5 per cent in the first month, which rose to 35.3 per cent in the second month. In the third month the increase was only 26.5 per cent. The other concentrations proved to be somewhat less effective. The 1:5,000 solution was least effective.

EXPERIMENTS WITH LANOLIN AND INDOLE-BUTYRIC ACID

A second series of experiments was devised to determine how much of the increase noted in the previous one was due to hormone stimulation

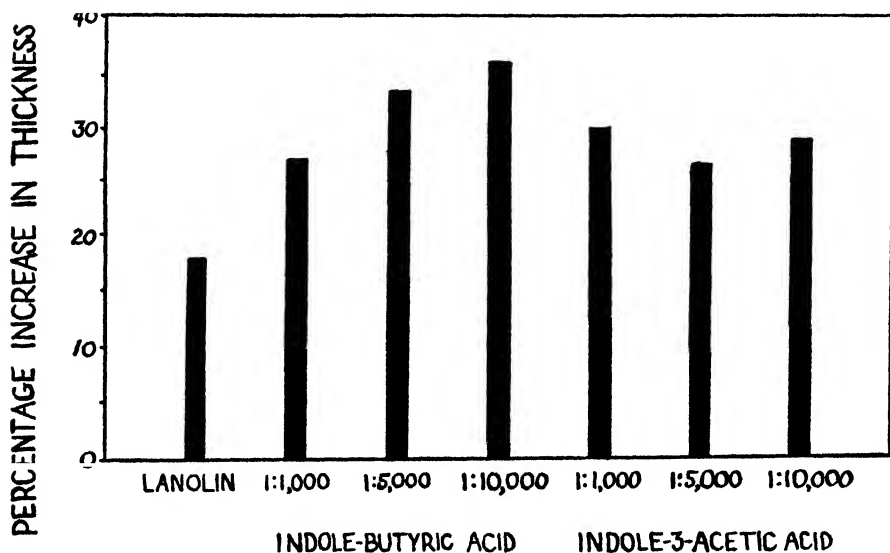


FIG. 2. Percentage increase of treated portion of panel over untreated (100 per cent) one month after treatment

and how much to the effect of the lanolin carrier in preventing desiccation. It was carried on for one month.

TABLE II

THE EFFECT OF LANOLIN AND INDOLE-BUTYRIC ACID ON BARK RENEWAL

In all these experiments the lower half of the panel was treated and the upper half served as a control. The figures give the bark thickness one month after treatment.

LINE D		LINE E	
Lanolin		1 : 5,000 indole-butyric	
<i>Tree</i>	<i>Mm.</i>	<i>Tree</i>	<i>Mm.</i>
1 Treated	6.7	1 Treated	7.2
Control	5.2	Control	5.3
2 Treated	8.2	2 Treated	8.1
Control	6.8	Control	6.4
3 Treated	5.8	3 Wind-damaged	
Control	4.8		
4 Treated	6.6	4 Treated	6.7
Control	6.0	Control	5.6
5 Treated	6.4	5 Treated	7.3
Control	6.0	Control	4.7
Average		Average	
Treated	6.74	Treated	7.33
Control	5.76	Control	5.50
Difference	0.98	Difference	1.83
Increase	17.0%	Increase	33.3%
LINE F		LINE G	
1 : 1,000 indole-butyric		1 : 10,000 indole-butyric	
<i>Tree</i>	<i>Mm.</i>	<i>Tree</i>	<i>Mm.</i>
1 Treated	8.1	1 Treated	7.4
Control	6.8	Control	4.7
2 Treated	7.3	2 Treated	9.1
Control	6.4	Control	7.3
3 Treated	7.6	3 Treated	7.1
Control	5.2	Control	5.4
4 Treated	8.6	4 Treated	7.4
Control	6.2	Control	5.4
5 Treated	6.7	5 Treated	7.7
Control	5.4	Control	5.8
Average		Average	
Treated	7.66	Treated	7.74
Control	6.00	Control	5.72
Difference	1.66	Difference	2.02
Increase	27.7%	Increase	35.3%

Pure lanolin and solutions of 1:1,000, 1:5,000, and 1:10,000 parts indole-butyric acid in lanolin were applied to the same clone, under the experimental conditions previously stated. The initial thickness of bark was one millimeter. The depth of renewed bark one month after treatment is shown in Table II.

Although lanolin alone increases the rate of renewal by 17.0 per cent, there is an additional stimulation due to the presence of the indole-butyric acid. This hormone is most effective at a concentration of 1:10,000, which gives an increase of 35.3 per cent or 2.02 millimeters one month after treatment. The relative percentage increment over the control is shown in Figure 2. The first-month increase in the previous experiment, which was due to the indole-3-acetic acid, is also shown for the sake of comparison.

DISCUSSION

Although the stimulating effect of indole-butyric acid becomes more marked as concentration decreases, this is not true of indole-3-acetic acid. Here the 1:1,000 concentration is most effective, at least in the early stages, and the 1:5,000 concentration shows the least effectiveness.

The effect of the lanolin is probably due to the fact that it protects the bark from desiccation, particularly during the dry season. Possibly this effect would not be so marked during the wet season.

SUMMARY

1. Experiments dealing with the effect of indole-3-acetic acid, indole-butyric acid, and lanolin on bark renewal are described.
2. The rate of renewal is most rapid in the first month after tapping.
3. Both the indole-3-acetic acid and the indole-butyric acid stimulated the rate of renewal.
4. Lanolin alone increased the renewal 17 per cent in the first month after application.
5. The treated zone of the panel exuded more latex when pierced by the bark gauge than did the untreated zone.
6. Indole-3-acetic acid is more effective at the highest concentrations used than at the lower concentrations, at least in the early stages.
7. Indole-butyric acid is most effective at the lowest concentrations used.

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The trunk of a rubber tree (*Hevea*), showing tapping panel, spout, and glass cup full of latex. Area of panel between *A* and *B* treated with hormone. Upper side of panel, beyond *A*, untreated

F O R E S T R Y

SOME RESUPINATE POLYPORES FROM THE REGION OF THE GREAT LAKES. XXI *

DOW V. BAXTER

IN 1922 the author began a survey of North American polypores. Since that time he has made field studies in every state of the Union, in Alaska, in every Canadian province as well as in the Yukon Territory, the Northwest Territories, and also in Labrador and Newfoundland (both of which have recently been annexed to Canada). In all reports of investigations and field expeditions (1) the title has been kept the same to preserve their unity and to facilitate references. It is the author's plan to incorporate in a volume on the resupinate polypores of North America the results of all these studies and to include additional data gathered since the publication of the various articles.

The present paper contains five reports on resupinate forms or pileate forms that have become resupinate.

The color terms given within quotation marks are those of R. Ridgway, *Color Standards and Color Nomenclature* (Washington, 1912).

Polyporus distortus (Schw.) Fr.

Abortiporus distortus (Schw.) Murr, Bull. Torr. Bot. Club, 31 : 422. 1904.

Boletus distortus Schw., Syn. Fung. Car., 71. 1818

Polyporus abortivus Pk., Bot. Gaz., 6 : 274. 1881.

* Throughout the work on these monographs I have been indebted to many individuals and institutions for suggestions, help, and privileges extended to me. Grants from the Horace H. Rackham School of Graduate Studies, of the University of Michigan, have greatly facilitated both the field and the laboratory studies. My appreciation is expressed particularly to the men who have accompanied me on my numerous expeditions to Alaska, the Yukon Territory, and the Northwest Territories, and to Newfoundland and Labrador. Much credit is due them for aiding in the collection and care of specimens and for living, at times, under rather difficult circumstances. I am under obligation to Professor T. G. Halle of Naturhistoriska Risk-muséet in Stockholm, with whom I have had the pleasure of association. Thanks are due several American institutions and scholars also. To the authorities at the New York Botanical Garden, to the staff of the Division of Pathological and Mycological Collections of the United States Department of Agriculture, to Dr. John Stevenson for Plates V and VI, and to Professor H. H. Bartlett, of the University of Michigan, I am especially indebted.

Polyporus rufescens (Pers.) Fr. ex Lloyd, but held distinct by Murrill, Bull. Torr. Bot. Club, 31: 422. 1904.

Fructification variable in growth habit, intertwined with roots and sticks or with central or lateral stem; stem often deeply extended and frequently tubercular to sclerotoid, extension which intertwines with decayed roots or wood, 8–12 cm. or more below the ground; pileus when developed 1–6 mm. thick, minutely but densely villose, “vinaceous buff”; context fibrous-tough, concolorous, duplex — the upper layer thin, the remaining radially fibrous; tubes 1–5 mm. long; mouths 0.5–3 to a mm.; spores¹ smooth, apiculate, ellipsoid to ovoid, 5–6 × 3.5–4 μ , chlamydospores 5–7 μ in diameter sometimes present, cystidia present or none, scarcely projecting beyond the hymenium; hyphae seldom branched, 4–8 μ in diameter.

Allied species. — The plant is described among the resupinate polypores since it may occur in a resupinate state about upright sticks. It suggests, for example, *Poria ambigua*, which at times may exhibit such a habit of growth. The pore mouths are similar in size, and the measurements of the spores for the two species overlap. There is no duplex context in *P. ambigua*, and the poria dries crisp and becomes so fragile that it is readily reduced to a powder between the fingers. *Pol. distortus* becomes harder upon drying.

As might be inferred from the similarity of names, resupinate forms of *Polyporus distortus*, which is especially variable in nature, may be mistaken for *Poria distorta* Murr. The tubes of *P. distorta* are given as shorter, being 1–2 to a mm. instead of 1–5 mm. long. Their mouths, too, are smaller. In *P. distorta* they are 4–5 to a mm., whereas in *Pol. distortus* the mouths are 1–3 to a mm.

Habitat. — *Acer Negundo*, *A. rubrum*, *A. saccharum*, *Ailanthus glandulosa*, *Betula nigra*, *B. papyrifera*, *Carya alba*, *C. illinoensis*, *Fraxinus* sp., *Juglans cinerea*, *J. nigra*, *Liriodendron Tulipifera*, *Magnolia grandifolia*, *Malus pumila*, *Plantanus occidentalis*, *Quercus alba*, *Q. palustris*, *Salix* sp., *Tilia americana*, *T. glabra*.

Distribution. — British Columbia, Ontario; Alabama, Arkansas, Connecticut, Delaware, District of Columbia, Florida, Illinois, Indiana, Iowa, Kentucky, Louisiana, Maryland, Massachusetts, Michigan, Missouri, Montana, New Jersey, New York, North Carolina, Ohio,

¹ Kauffman noted that in immature specimens or arrested-growth forms the pileus is a mass of pores filled with spores. Portions, at least, produce numerous conidia borne singly on slender sterigmata where present. The conidia are subglobose, and are about 10 μ in diameter.

Oregon, Pennsylvania, Tennessee, Texas, Virginia, Washington, Wisconsin.

Occurrence. — This plant may not always be wood-inhabiting, for it grows frequently about stumps and trunks of deciduous trees in low wet places. Kauffman found it around poison ivy roots and noted it in basswood and maple woods.

Cultures. — Isolated by Davidson, Campbell, Blaisdell (5). The fungus causes a positive reaction to tannic acid medium.

Trametes mollis (Sommf.) Fr., *El.* 71. 1828;

Hymen. Eur. 585. 1874

Antrodia mollis (Sommf.) Karst. in Medd. Soc. pro Fauna et Flora Fenn., 5 : 40. 1879.

Daedalea mollis (Sommf.), Suppl. Fl. Lapp., p. 271. 1826.

Polyporus cervinus Pers., Myc. Eur., 2 : 87. 1825 (non *Trametes cervina* (Schw.) Bres., 1903.)

Polyporus mollis (Schw.) Kroh et Almqu., Svensk. Fl., 2nd edition, 5 : 274. 1932 (teste Pilát, 1936) (non *P. mollis* Fr., 1 : 360. 1821; nec Persoon, Myc. Eur., 2 : 62. 1825).

Trametes cervina (Pers.) Lloyd, non *Boletus cervinus* Schweinitz, Schriften Nat. Gesell., Leipzig, 1 : 96. 1822. (*P. cervinus* Fries, Epicr., 474. 1838; *Trametes cervinus* Bres., Ann. Myc., 1 : 81. 1903.)

Trametes stereoides (Fr.) sensu Bres. in Atti Ac. Agiati, III, 3 : 92. 1897. Shope in Ann. Mo. Bot. Gard., 18 : 367. 1921 (non *Polyporus stereoides* Fr., 1831).

Important specimen:

Trametes mollis Sommf., East Berne, Adirondack Mts. Leg. C. H. Peck (*Pol. cervinus* Pers.). Herb. N. Y. State Museum.

Fructification coriaceous, sessile, but more often effused-reflexed or resupinate, reflexed part conchate, $0-2 \times 1-9 \times 0.1-0.3$ cm.; surface tomentose, zonate, brown, "Saccardo's umber" to "sepia"; margin thin, concolorous, becoming revolute; context 1 mm. or less in thickness, "cinnamon buff"; tubes up to 4 mm. long, concolorous with the context; mouths variable in shape, poroid, often becoming sinuous or daedaloid, 1-2 to a mm., "pinkish buff," "cinnamon buff" to "Saccardo's umber," spores hyaline, smooth, cylindric, $9-12 \times 3.5-4.5$ (Shope).

Allied species. — *Trametes mollis* (Sommf.) Fr. resembles *Trametes variiformis* closely. I suspect that, if specimens of *T. variiformis* were found in Europe, they might receive the name *T. mollis*, just as some coniferous collections have been so labeled in this country. The spores of the hardwood-inhabiting *T. mollis* (Sommf.) Fr. ($7-10 \times 2.5-3.5 \mu$) are about the same as those of the coniferous fungus *T.*

variiformis ($6-8 \times 2.5-3 \mu$). The tubes of *T. variiformis* are generally longer, but this character is only relative. The context of *T. variiformis* is duplex, the upper layer being concolorous with the surface, whereas in *T. mollis* the context is pale brown or clay color.

T. campestris Quél. is also closely allied, since it may resemble *T. mollis* in general appearance. The spores of *T. campestris*, however, are large ($10-15 \times 4.5-5.5 \mu$ Pilát).

Romell (16) discusses a specimen of *Pol. stereoides* with pore mouths 4-5 to a mm. (Lapland). Its habit resembles that of a *Stereum*. The plant agrees with an authentic specimen from Femsjö in the herbarium of Fries. It is believed that Elias Fries either "suggested the name or at least approved it." Romell adds: "There is, however, another authentic specimen (with a label written by El. Fries), but this belongs to *Pol. cervinus* Pers." For the record Romell keeps this *Pol. cervinus* (*Daedalea mollis* Sommf., *Trametes mollis* Fr.) separate. According to him, it is "a species which is really closely allied, though in my opinion specifically distinct, as it is *much thicker and has pores more than twice as large and consequently a different habit*, and no intermediate connecting forms exist." *Pol. stereoides* is regarded as a northern plant and one never seen by Romell but in Lapland.

Difficulty has also been created by calling other and unrelated plants "mollis." Among these are certain more fragile polypores which are slightly red or which become reddish upon bruising or drying. *Pol. mollis*, for example, a soft, watery species when fresh, becomes rigid and red or pink when dry (17). It is an entirely different plant from *T. mollis*.

Irpex mollis should not be mistaken for *Trametes mollis*. *I. mollis* B. & C. is characterized by long (1 cm. or more) white teeth. The entire pileus is large and thick, remaining white or cream color in contrast to the browns exhibited by *T. mollis* (Sommf.) Fr.

Habitat. — *Acer circinatum*, *A. pennsylvanicum*, *A. saccharinum*, *A. saccharum*, *A. spicatum*, *Alnus rubra*, *Betula lutea*, *B. papyrifera*, *B. papyrifera kenaica*, *Fagus grandifolia*, *Fraxinus americana*, *Ostrya virginiana*, *Picea Engelmannii*, *Pinus Strobus*, *Populus balsamifera*, *Quercus alba*, *Q. Garryana*, *Q. phellos*, *Salix sp.*, *Sambucus cœrulea*, *Ulmus americana*.

Distribution. — Alaska, Northwest Territories; British Columbia, Labrador, Nova Scotia, Ontario, Quebec; Arizona, California, Colorado,

Idaho, Illinois, Kentucky, Maine, Michigan, Montana, New Hampshire, New Jersey, New York, North Carolina, Ohio, Oregon, Pennsylvania, Rhode Island, Tennessee, Texas, Vermont, Washington, West Virginia.

Cultures. — Isolated by Davidson, Campbell, and Blaisdell (5), who report that the fungus gives a strong positive reaction to tannic acid medium.

Poria subserpens Murr., *Lloydia*, 10: 245–246. 1947

(Plates I–III)

Trametes subserpens Murr., *Mycologia*, 12: 107–108. 1920.

Trametes serpens Auct. Am., but Lloyd only pro parte (some determinations made by Lloyd are *Poria papyracea*, and not *Trametes subserpens*).

Elmeriana setulosa (P. Henn.) Bres., Philippines (?), teste Murr., *Mycologia*, 12: 108. 1920

Poria setulosa P. Henn. (?), teste Murr., *Lloydia*, 10: 246. 1947.

Type and important specimen observed:

Trametes serpens Fr., "orig. ex." Fries. Femsjö, Sweden. Herb. of Bresadola, Stockholm.

Fructification white, pallid, or cream, corky, appearing in patches frequently about 4×3 cm., but becoming widely effused for as much as one or two meters, sometimes curled at margin but mostly resupinate, averaging 1 mm. in thickness; margin up to 1 mm. wide, "light buff"; tubes often arranged obliquely, 1–2 mm. long; hyphal pegs in tubes visible under hand lens (Overh.); mouths 1–2, mostly 2, to a mm., concolorous with the margin; dissepiments thick; spores $8\text{--}10 \times 3.5\text{--}4.5 \mu$; hyphae $2\text{--}2.5$ (3) μ in diameter.

Allied species. — *Poria subserpens* is one of the most distinctive of the resupinate polypores of the Gulf states. There has been some confusion about the name that should be applied, but no closely related species exist in continental North America. The name *P. straminea* Bres., designating a plant of the Philippines, has been variously interpreted, and some of the versions have been so broad as to include *P. subserpens*. Likewise, *P. setulosa* P. Henn. of the Philippines resembles *P. subserpens*.

Poria subserpens and *Trametes sepium* may be confused since both are coriaceous; they may resemble each other in color and in size of pore mouths. The dissepiments between the mouths are thick in both, and the two polypores are frequently entirely resupinate. The spores of *P. subserpens* are $8\text{--}10 \times 3.5\text{--}4.5 \mu$, and those of *T. sepium* are $8\text{--}14 \times 3.5 \mu$.

Poria subserpens is apt to be whiter than *Trametes sepium*. Furthermore, the relatively thin margin of *P. subserpens* is more likely to become upturned upon drying, with the tube layer remaining definitely resupinate. Drying affects *T. sepium* but little, and the margin in fresh plants becomes more effused-reflexed or even pileate in form, the pilei being often nodulose. A nodulose appearance is never evident in *P. subserpens*.

The two species, however, may be readily distinguished in culture by the fact that buff-colored pores are formed by *Trametes sepium* on both hardwood and coniferous blocks in one-year-old tests, whereas no pore formation takes place on either red gum or white pine in cultures of *Poria subserpens*.

Specimens of *Trametes serialis* may be mistaken for those of *Poria subserpens*. In nature *T. serialis* is chiefly a conifer-inhabiting fungus, whereas *P. subserpens* occurs on hardwoods.

Since resupinate specimens of *Fomes fraxinophilus* are corky, white or whitish, and possess a white to light-brown context, and since the mouths of the tubes average 2-3 to a mm., some difficulty may be encountered in separating it from *Trametes subserpens*. *F. fraxinophilus* grows on standing trunks, whereas *T. subserpens* is mostly, if not always, on logs. The spores of *F. fraxinophilus* are ellipsoid to ovoid, measure $6-8 \times 5-6 \mu$ (Lowe), and are not cylindric-ellipsoid, as in the species of *Trametes* discussed.

Some specimens of *Poria subserpens* might suggest those of *Trametes mollis* (Sommf.) Fr., which is never as white as most specimens (and all freshly growing plants) of *P. subserpens*. The margins of the two species are characteristic. At least, *T. mollis* is more often effused-reflexed, the surface of the pileus being tomentose, zonate, and brown. *P. subserpens* is usually more extensively effused over the substratum and often extends over the log for several feet. *P. subserpens* is mostly southern in its range and is common on Liquidambar and Lyssa. *T. mollis*, on the other hand, is mostly northern and is usually on species of Populus and Alnus. Both fungi, however, attack other woods.

Habitat. — *Acer floridanum*, *Carpinus* sp., *Carya* sp., *Celtis* sp., *Citrus aurantium*, *Ficus* sp., *Fraxinus americana*, *F. pennsylvanica lanceolata*, *Gleditsia aquatica*, *Liquidambar styraciflua*, *Lysiloma bahamensis*, *Nyssa aquatica*, *N. biflora*, *Persea americana*, *Pinus echinata*, *Planera aquatica*, *Populus* sp., *Quercus laurifolia*, *Q. Shumardii*, *Q. virginiana*, *Salix nigra*, *Ulmus* sp., *Vitis* sp.

Distribution. — Alabama, Florida, Georgia, Illinois, Kentucky, Louisiana, Mississippi, North Carolina, New York, Ohio, Oklahoma, Pennsylvania, South Carolina, Tennessee, Texas, Virginia.

Occurrence. — *Poria subserpens* is one of the most common resupinate polypores of the states bordering the Gulf of Mexico. It is especially abundant on hardwood logs in tupelo-gum swamps. *Nyssa aquatica* is the usual substratum, but *Liquidambar Styraciflua* is frequently attacked.

Cultures. — Isolated from *Quercus Shumardii*, Fort White, Florida, and from *Nyssa biflora*, Stark, Florida. The snow-white mycelium from both isolates exhibits a concentric to radiating type of growth in malt-agar cultures in petri dishes. The two isolates are similar in their growth habits on wood, the mycelium covering both red-gum and white-pine test blocks in one-year-old flask cultures.

Poria subserpens grows faster in the dark than in the light. It also belongs to the rapid-growth group and in the category "high temperature" for optimum growth.² The white to "cartridge-buff" or "cream-buff" mycelium covers hardwood blocks (red gum), and eventually radiates in strands or fanlike growth over white-pine blocks, but often does not cover such wood as densely in one-year-old cultures. No pore formation has occurred.

Cultures exhibit a strong positive reaction to tannic acid medium.

Fomes subroseus (Weir) Humphrey and Siggers,
Journ. Agric. Res., 47: 999. 1933

(Plate IV)

Fomes carneus (Nees) Cooke, Grevillea, 14: 21. 1885.

Fomes Palliseri Berkeley, Grevillea, 10: 98. 1882. Saccardo, Syll. Fung., 6: 204. 1888.

Fomes carnea granularis Pk., teste Pilát, 1936.

Fomes carnea subzonata Pk., teste Pilát, 1936.

Polyporus carneus Nees, Nova Acta Nat. Curiosorum, 13, t. 3. 1827.

Trametes subrosea Weir, Rhodora, 25: 217. 1923.

Trametes arctica Berk., Herb., teste Pilát, 1936.

Trametes carnea (Nees) Pilát, Bull. Soc. Myc. Fr., 48: 19. 1932.

Trametes carnea Cooke (sense of American students only).

Fructification annual or perennial, sessile, effused-reflexed, usually thin, coriaceous, 2–6 × 2–15 × 0.5–2 cm. (Shope), or resupinate; surface of pileus zonate or azonate, velvety tomentose, "pale drab gray," "wood brown" to blackish behind, becoming radially appressed, fibril-

² The terms used to represent various categories for growth are defined in Paper V (19 [1934]: 305–312) of this series.

lose, or glabrous; margin thin, sterile below, "light mouse gray," "light cinnamon drab"; context 1–5 mm. thick, corky, "fawn color," tubes concolorous, 0.5–4 mm. long each season; mouths "pale Quaker drab," "light gray vinaceous" to "russet vinaceous," concolorous, 3–5, mostly 4–5, to a mm.; basidia hyaline, $5-6 \times 10-20 \mu$ (Pilát); spores hyaline, smooth, cylindric, sometimes allantoid, $6-8 \times 2-2.5 \mu$; no cystidia, hyphae seldom branched $3-5 \mu$ (Shope) in diameter.

Forms.—*Trametes arctica*, listed here as a synonym, is regarded by Lloyd (10) as a form of *F. subroseus arctica* (Berk.) Lloyd with the surface silvery white and with appressed fibrils. The name *Pol. Palliseri*, also listed here as a synonym, was likewise applied to this plant by Berkeley.

Pilát keeps the name *Trametes carnea* and refers to the plant as *T. carnea* (Nees) Pilát. In view of the extensive use of the species name *subroseus* in pathological literature by Weir (24) and others (22, 25) and in view of the fact that *Trametes* is a doubtfully practical genus, it seems unwise to return to the use of the name *carnea*.

Allied species.—*Fomes subroseus* is most closely allied to *F. roseus*. The types of rot produced are indistinguishable. Although the pilei of *F. subroseus* are mostly thin, specimens are found occasionally that resemble the more ungulate types of *F. roseus*. The color of the mycelium of both species varies from white to pink, and the odor of cultures of the two is that of green apples. Nevertheless, the two polypores are distinct in their growth features and may be separated not only on the basis of their rates of development but also on optimum growth temperatures. (See page 51.)

Mounce and Macrae (12) found that both *Fomes subroseus* and *F. roseus* are heterothallic and bipolar with one exception, and that complete interfertility exists between haploid mycelia derived from different sources. The exception is of particular interest because it shows that two cultures of *F. subroseus* from widely separate sources possess one interfertility factor in common. These authors state that the two fungi may be differentiated on the basis of their spore characters. According to them, the failure to obtain clamp connections in any of the many pairings of a haploid mycelium of *F. subroseus* with a haploid mycelium of *F. roseus* only serves to emphasize that these two fungi are distinct.

Separation of *Fomes subroseus* from *F. roseus* on the basis of growth at certain temperatures has been made by Snell, Hutchinson,

and Newton (22). A test at 30° C. or 32° C. differentiates these two. *F. subroseus* grows over 32 mm. at 30° C., whereas *F. roseus* grows only about 24 mm. at this temperature. Evidence (22) is also presented to show that the two vary in moisture requirements, or in dryness tolerances with regard to fruiting. *F. roseus* is found in drier places, often on dry hewn timbers, but *F. subroseus* usually grows on logs covered with bark or on wood in situations that are decidedly moist (Pl. IV). *F. roseus* also occurs on worked timbers in the open and on decorticated bolts on top of log piles in well-ventilated places. *F. subrosea*, on the other hand, grows in low places and in parts of the pile protected from drying by grass and ferns.

Points of difference between the two species, *Fomes subroseus* and *F. roseus*, may be summarized as follows:

Fomes subroseus

1. Rate of growth in culture comparatively fast.
2. Optimum growth temperature 28°–32° C. with most probable value at 31° C.
3. Inhibiting temperature 38° C.
4. Requires moist sites with high humidities.
5. Spores narrow, cylindrical, slightly curved, allantoid, $4-7 \times 1-2 \mu$; smaller than those of *F. roseus*.
6. Fruiting bodies generally longer and thinner than those of *F. roseus*.
7. In general, no clamp connections form in pairings of a haploid mycelium of *F. subroseus* with one of *F. roseus*.

Fomes roseus

1. Rate of growth in culture comparatively slow.
2. Optimum growth temperature 28° C.
3. Inhibiting temperature 35° C. (22).
4. Requires relatively drier sites than *F. subroseus*.
5. Spores elongate-ellipsoid, $5-7 \times 2.5-3.5 \mu$; larger than those of *F. subroseus*.
6. Fruiting bodies generally thicker and less elongate than those of *F. subroseus*.
7. In general, no clamp connections form in pairings of a haploid mycelium of *F. roseus* with one of *F. subroseus*.

The European species, *Polyporus albocarneogilvidus* sensu Romell, might possibly suggest *F. subroseus* if only a small specimen without a part of the substratum were available for observation. *Pol. albocarneogilvidus* is *Trametes*-like. The mouths of the tubes are tinted slightly rose, and the fungus forms rather large coriaceous sheets, that is, they are often entirely resupinate.

Polyporus albocarneogilvidus is common around Stockholm on oak, and I have frequently observed it on dead limbs still attached to the trees. The habitat, the substratum, the color (which is not so distinct as in *F. subroseus*), and the larger mouths of this European polypore

should readily enable one to distinguish it from *T. subrosea*. I have never seen this European plant in America. The name *Poria micans*, as used by Bresadola with reference to some collections of *Pol. albo-carneogilvidus*, is not acceptable.

Fomes subroseus Feei (*Trametes Feei* Fr.) (Pl. V, Fig. 1) is a tropical plant much like *Fomes subroseus* in size, shape, and color. The fibrillose surface, which is the only distinction between the two, is not always in evidence, and Lloyd (10) states that the two plants merge into each other. Snell, Hutchinson, and Newton (22) report as a result of their tests in comparing *F. roseus*, *T. subrosea*, and *T. Feei* that *T. Feei* in culture grows more slowly at all temperatures and is inhibited from growing at a lower temperature. It could be differentiated from the other two fungi if grown from 30° to 34° C. The type came from Brazil, and this is apparently the common plant of this group from Brazil. It is reported by Sharp (19) from Mexico and Guatemala.

Trametes Sagraeana, named by Montagne from Cuba, resembles *T. Feei*, though Lloyd (10) points out that most of Montagne's species under this name are *Trametes cupreo-rosea*.

Trametes Sagraeana has a smooth, soft, dull surface and smooth and very minute pores. It differs from *T. Feei*, according to Lloyd, in its more punky context and in having a surface soft to the touch, not hard and fibrillose. Lloyd finds *T. Sagraeana* rare in the West Indies (and believes the several collections from West Indies so referred at the New York Botanical Garden to be *T. cupreo-rosea*). He also states the abundant specimens so referred to by Murrill from Cuba are *T. Feei*.

Trametes cupreo-rosea (Pl. V, Fig. 2) is thin and rigid and is attached by a reduced base ($6 \times 9 \times 0.5$ cm.). The surface is striate-fibrillose, pale rosy color (buff pink). The context is thin and hard. The pores are round, medium to large, mostly about 0.5 mm. in diameter, with thin walls; tissue concolorous (10). Lloyd reports that a number of specimens from Brazil are at Kew, and there is a collection from Malay. He states that he has never seen a specimen from the West Indies. A collection of this fungus from Coconut Grove, Florida, is in the Farlow Herbarium, Harvard.

Trametes lilacino-gilva (Pl. VI), according to Lloyd, is in the genus *Fomes*, is the Australian analogue of *T. Feei* of American tropics, and has about the same color and surface. It differs in having notably larger pores and a more strongly fibrillose surface. The Aus-

tralian forms all have larger pores than the analogues in the American flora.

Trametes Eucalypti is, according to Lloyd, probably an Australian form of *T. lilacino-gilva* as to color and pores, but has an even pileus corresponding to that of *T. subrosea*.

Trametes roseola is an African species, close to *T. plebeia* in color, but differs in context. The surface is dirty rose, not zoned, and is slightly rugulose. The context is punky, dry, pale salmon ("light ochraceous salmon"). The pores are minute, rigid, 1–2 mm. long, and the spores are globose 4–5 (10).

Trametes plebeia in New Zealand, Indian, and Philippine plants has pinkish-cinnamon context, surface, and pore mouths. The surface of the fruiting body is smooth, dull, minutely velutinate, and soft to the touch; the context is hard and rigid (10). Lloyd (10) reports that Berkely referred the species to *T. plebeia* var. *cubensis* (*Polyporus supinus*) of American tropics, which is not a variety and has no analogy to it.

Habitat. — *Abies balsamea*, *A. grandis*, *Alnus rubra*, *Arbutus Menziesii*, *Betula occidentalis*, *B. papyrifera*, *occidentalis*, *Chamaecyparis thyoides*, *Juniperus virginiana*, *Larix laricina*, *L. occidentalis*, *Picea Engelmannii*, *P. excelsa*, *P. glauca*, *P. mariana*, *P. rubra*, *Pinus Banksiana*, *P. contorta*, *P. monticola*, *P. palustris*, *P. ponderosa*, *P. resinosa*, *P. rigida*, *P. strobiformis*, *P. Strobilus*, *P. taeda*, *P. virginiana*, *Prunus amygdalus*, *P. pennsylvanica*, *P. persica*, *P. serotina*, *Pseudotsuga taxifolia*, *Quercus borealis maxima*, *Taxodium distichum*, *Thuja occidentalis*, *Tsuga canadensis*, *T. heterophylla*.

Distribution. — Northwest Territories; Alberta, British Columbia, Manitoba, New Brunswick, Newfoundland, Nova Scotia, Ontario, Quebec, Saskatchewan; Alabama, Arizona, California, Colorado, Connecticut, Delaware, District of Columbia, Florida, Georgia, Idaho, Illinois, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Montana, New Hampshire, New Jersey, New Mexico, New York, North Carolina, Oregon, Pennsylvania, Rhode Island, South Carolina, Tennessee, Vermont, Virginia, Washington, West Virginia, Wisconsin.

Occurrence. — *Fomes subroseus* is apparently unknown in Europe. It grows in most sections of the northern United States and Canada. It is not common in Newfoundland, but in general it is most frequent in areas north of the states that border the Gulf of Mexico.

The occurrence of *Fomes subroseus* in the field with reference to

that of its closely related ally, *F. roseus*, is significant. *F. subroseus* is most likely to grow on "unworked" timber in which moisture is more plentiful, as in moist log piles it is protected from drying out. *F. roseus*, on the other hand, occurs most frequently on "worked timbers," or on top of piles not so protected (22).

The occurrence of *F. subroseus* on *Prunus* in Oregon, where it causes much rot in stone-fruit trees, is added evidence of Davidson and Campbell's observation (4) that many normally coniferous species occur on *Prunus* among the hardwoods.

Cultures. — Isolated from tamarack, Whitmore Lake, Michigan. The fungus is characterized by a white to "shell pink" mycelial growth in culture. Some cultures remain almost white, whereas others may be slightly pink, or streaked with pink or "hazel" to "pecan brown" or "Rood's brown." Poroid areas form in wood-block cultures and appear often on malt-extract agar in petri-dish tests after two weeks. Basidiospores are produced. A few chlamydospores are formed, and clamp connections appear in abundance.

No reaction is exhibited on tannic acid medium.

The growth of *F. subroseus* may be considered moderately rapid and, in contrast with that of *F. roseus*, is so much faster at 31° C. that the two fungi may be distinguished on the basis of different growth rates (22).

Fomes subroseus belongs to the class of fungi that grow more rapidly in the light.

An isolate, reported by Humphrey and Siggers (8), exhibited an optimum temperature for growth at 28° C. The inhibiting temperature was 38° C. The fungus is placed, therefore, in their "intermediate-temperature" group (optimum between 24° and 32° C.).

The effect of moist heat and dry heat upon *Fomes subroseus* in three-quarter-inch wood-block cultures has been tested by Snell (21). This fungus was unable to withstand 131° F. (55° C.) for twelve hours at moist heat, whereas it took 221° F. (105° C.) twelve hours to kill the fungus with dry heat.

Reaction to chemicals. — Certain water-soluble extracts are toxic to *Fomes subroseus*. Water-soluble extract from western red cedar in concentrations of 4 per cent or over greatly retarded the growth of this fungus, according to tests made by Southam and Ehrlich (23).

Resistance of *Fomes subroseus* to sodium fluoride has been tested by Richards (15) and has been compared in its resistance to a num-

ber of other wood-destroying fungi. Beginning with the least resistant and ending with the most resistant, the list that follows indicates the relative position of *F. subroseus*: *Poria incrassata*, *Polystictus abietinus*, *Pol. versicolor*, *Fomes roseus*, *F. pinicola*, *F. subroseus*, *Lenzites saepiarum*, *Polyporus hirsutus*, *Fomes Pini* var. *Abietis*, *F. annosus* (possibly *Polyporus tulipiferus*, identity not certain), and *Lenzites trabea*.

Decay. — The rot caused by *Fomes subroseus* in conifers is identical with that brought about by *F. roseus*. In the incipient stages the wood turns somewhat darker than when sound, but the decayed parts are lighter in color than the brown to be observed in advanced stages of rot (7). Usually pink to red-brown patches appear in more or less elongated areas. These coalesce so as to form larger regions of decay. The wood shrinks on drying and breaks up into cubes.

In juniper there is at first a slight change from red to brown over a considerable area. As the discolorations deepen, fissures begin to appear. Pocket-like areas are formed about the fissures by the shrinkage of the wood on their periphery. Sometimes firm hard wood separates the punky portions and resists further decay. The pockets are most common near the base of the host, and here they often coalesce to form large irregular cavities filled with the brown charcoal-like wood. Overmature trees may be almost hollow at the base. Such specimens may be wind-thrown when the hollow becomes so great that the ring of sapwood cannot adequately support the tree.

In addition to causing rot in conifers, *Fomes subroseus* attacks peach and prune trees. The brown rot has been demonstrated to have been produced by the cytohydrolytic enzymes lignase, cellulase, and hemicellulase. Emulsin, also present in the mycelium, makes available the products from glucoside digestion in the wood (25).

Importance. — Comparatively few fungi which occur on structural woods attack both coniferous and hardwood trees as standing timber. *Fomes subroseus* is a conspicuous example of one fungus that does attack hardwoods and conifers, both living and fallen.

In the East it is commonly regarded as a scavenger fungus on dead coniferous wood, but if it occurs on pulpwood, the damage caused may be greater.

Frequently living junipers are attacked by *Fomes subroseus*, which produces a heartrot in them as well as in *Chamaecyparis thyoides*. A brown cubical rot appears in trees attacked (3).

Losses in prune orchards are large but difficult to evaluate. The damage to the diseased tree is not limited to the heartwood, since the sapwood is attacked. This results in destroying the water-conducting power by reducing the volume and by the stimulation of the growth of tyloses in the xylem vessels (25). Such disturbances give rise to "drouth effects" in the affected tops.

Zeller (25) conducted a survey of prune orchards to determine the extent of damage caused by *Fomes subroseus*. Of 1,261 prune trees in orchards having average horticultural care, 1,212 showed heartrot. Of these, 885 (or 73 per cent) were decayed by *Fomes subroseus*. The pruning cut in 619 (or approximately 70 per cent) of these decayed trees was two inches or more in diameter.

In some localities within the active range of the fungus vigorously growing older orchards do not seem to be affected by heartrot. The lack of heartrot in many orchards seems to be related to the system of pruning adopted by the grower.

Control and prevention in orchards. — In general, heartrot caused by *Fomes subroseus* is less prevalent in prune orchards where the system of pruning used eliminates operations on the main leader branches and trunk, particularly if trees are so trained in early years that the removal of large branches is unnecessary later. Wounds should be treated with an antiseptic dressing, such as Bordeaux paint, made by mixing linseed oil into a Bordeaux dust until a thick, smooth paint is formed (25).

Control and prevention in the forest. — Older trees are more susceptible than younger ones, so that cutting in relatively short rotations should be effective. For Tennessee juniper, Von Schrenk (18) estimated that, if cuttings are made between 65 and 70 years (when the trees average about 12 inches in diameter), substantial control of *Fomes subroseus* will result.

Though coniferous logs are usually removed from the woods soon after cutting, it is necessary at times to store them there. Care in woods storage becomes an especially important problem when large amounts of timber are felled by catastrophic storms (2). Complete submersion of the wood in fresh water before the decay fungus starts prevents rot, but damage from marine borers may result if the water is tidal or brackish. Deep submersion involves, however, high costs of recovery of the logs, and should therefore be avoided (2).

For storage of coniferous pulpwood in the forest, peeling delays

the action (9) of such a fungus as *Fomes subroseus*, and if the sticks are stacked on ends in open piles (and preferably off the ground), as is done frequently in Sweden, there will be less decay. Immediate peeling prevents bark beetles and wood borers from laying eggs in the wood, and this practice tends to reduce the incidence of rot. Such a procedure to delay fungus action may be especially justified financially if the wood is to be floated to the mill, a method used in some areas in North America. Debarking increases buoyancy of the wood.

In the North pulpwood is often cut in small lots and allowed to accumulate in the woods or at the point of shipment until a sufficient amount is obtained for selling in larger units. It may be stored for as much as two years before shipping, a practice that favors the development of *Fomes subroseus*. Upon arrival at the mill this wood is often handled like recently felled timber and thrown in with freshly cut sticks, so that additional losses from storage of all wood in the piles may be sustained. Such a practice should be avoided.

Control and prevention at the mill and in use. — In North America pulpwood is stored (a) in water, (b) on the ground in huge conical piles, and (c) in ricks. Water storage prevents decay if the wood is immersed. Log parts above the water level may decay if they remain in the same position for long periods. In the conical piling conditions are usually favorable for decay in the interior of the pile. Wood that has been water-transported from the forest to the mill can be protected from rot (and fire) by a system of overhead water sprays so regulated as to keep it soaked beyond the point favorable for fungus activity. It is impossible to soak dry wood in the piles to such an extent that decay will be prevented throughout the cones. Likewise, spraying of ricked wood, even if both ends of each log are exposed to the direct action of the water, is not generally satisfactory.

As a measure of rot prevention ricking pulpwood in piles raised from the ground on concrete or treated skids or piers is preferable to conical piling. The ricks should be separated by open spaces to allow ventilation. Yard sanitation is always necessary and, regardless of method of piling, the oldest wood in the lot must be used first.

In the South pulpwood deteriorates so rapidly that in general large quantities are not stored for more than four or six weeks. Often the fresh sticks are conveyed directly from barge, railroad car, or truck to the chipping machines.

The possibilities of reducing the activities of fungi in wood used in

buildings has been considered. *Fomes subroseus* belongs to the "intermediate temperature" or the "high-temperature" group that includes *Lenzites saepiaria*, *L. trabea*, and *Trametes serialis*. Hoxie (6) debated the possibility of using heat to retard the development of the comparatively "low temperature" or "dry-rot" fungi in buildings. It was concluded by Snell (21) from culture-block tests (see section entitled "Cultures") that, since a heating system could not supply a temperature much above 125° F., heating practices could not be effective in controlling *F. subroseus*. Too high a temperature for too long a period would be necessary to kill the fungus within the wood. Even for fruit-cannery buildings and other such structures of moist occupancy the heat required to kill such a species as *F. subroseus* or other species in this group could not be satisfactorily obtained. Dry heat, applied occasionally for the purpose of drying out the wood, is, nevertheless, to be recommended.

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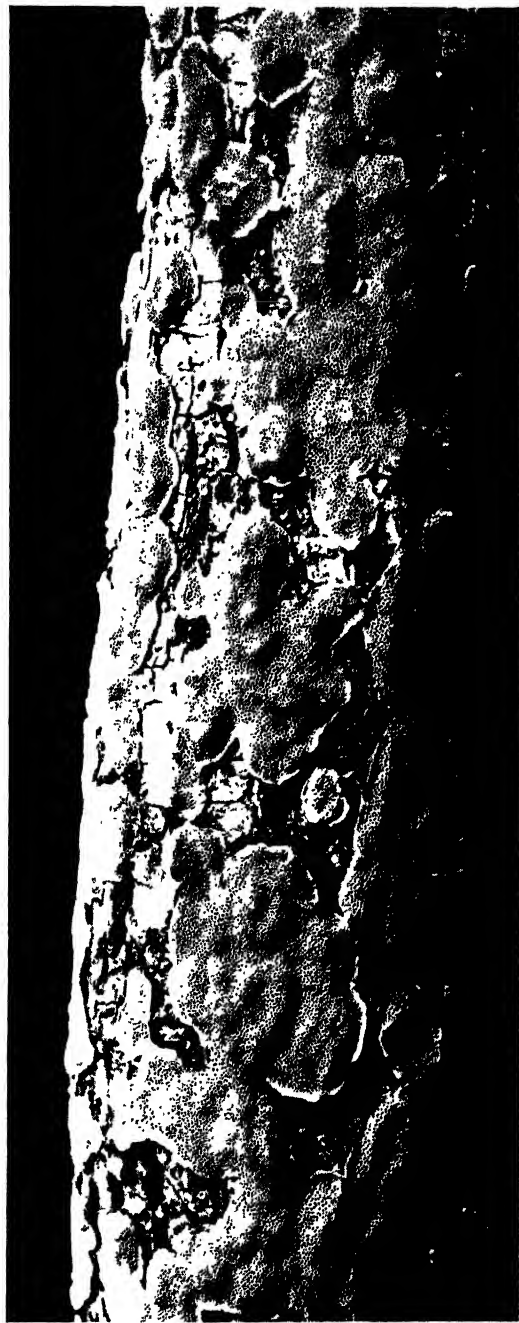
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PLATES I-VI

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PLATE I



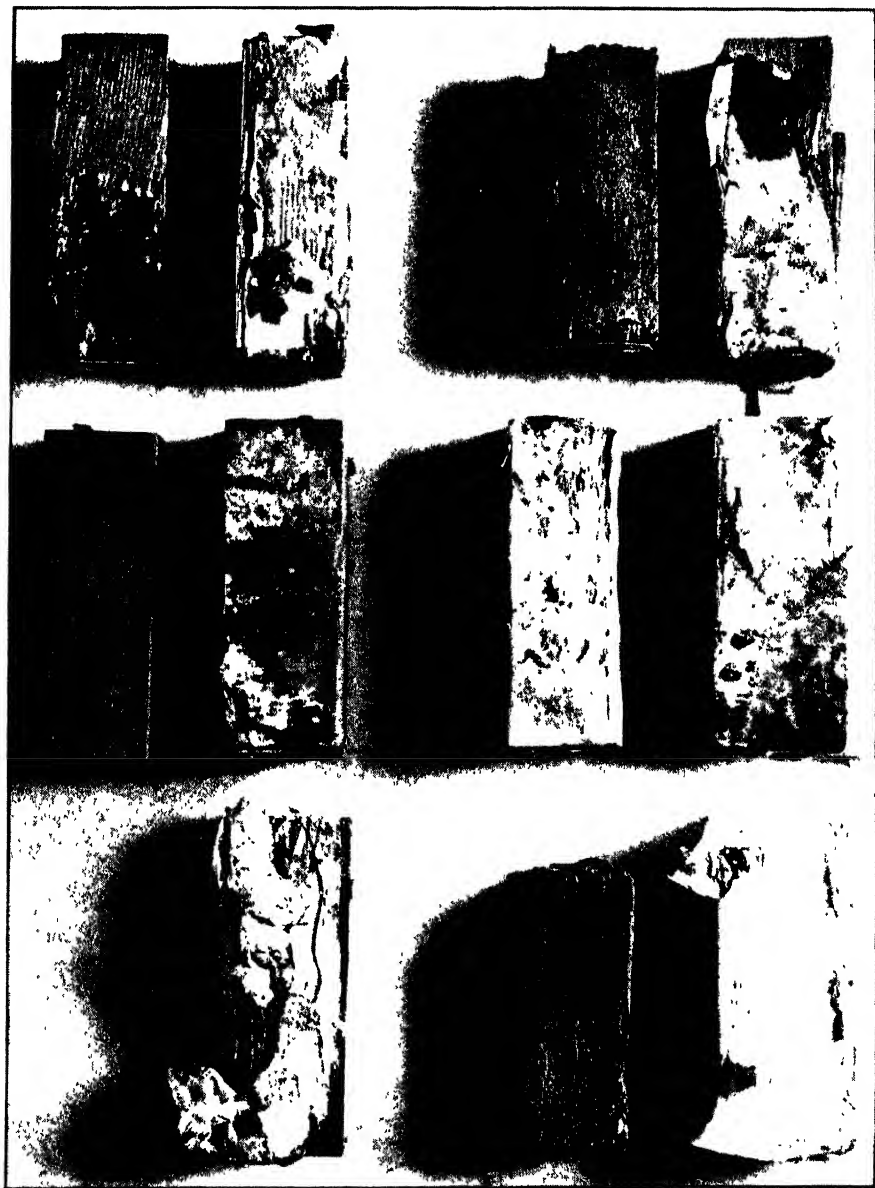
Trametes subserpens on *Nyssa biflora*, Start, Florida

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PLATE II



Portia subserpens on *Liquidambar styraciflua*, Dismal Swamp, Virginia



Trametes subserpens, normally on southern hardwoods, but grows well on both white pine and red gum in culture. White pine blocks to left of center; red gum blocks to right. Top row Isolate from *Nyssa biflora* Middle row Isolate from *Quercus shumardii* Bottom row. Isolate from *Carpinus* spp



Fomes subroseus on spruce. Winchendon, Massachusetts



FIG 1



FIG 2

FIG 1. *Trametes Fect*, Rio Grande du Sol, Brazil. 51788 Lloyd collection, Beltsville Maryland. Morphologically this tropical plant appears to be similar to *Fomes subroseus*, but it grows more slowly at all temperatures. It can be further differentiated from *F. subroseus* and *F. roseus* if grown at temperatures from 30° to 34° C.

FIG 2. *Trametes cupreo-rosea*, Bahia, Brazil. 17497 Lloyd collection, Beltsville, Maryland. This tropical plant has a thin pileus and is attached by a reduced base. A specimen so named from Florida is to be found in the Farlow Herbarium, Harvard.



Trametes lilacino-gilva, East Caulfield Australia 45652 Lloyd collection, Beltsville, Maryland. Lloyd regarded this plant as the "Australian analogue" of *Trametes Feei* of the American tropics. This fungus needs to be compared with *T. cupreoro-sea*, *T. Feei*, and the other named species and forms in this group

RED PINE AND THE EUROPEAN PINE-SHOOT MOTH IN SOUTHERN MICHIGAN *

PAUL O. RUDOLF

RED PINE (*Pinus resinosa*) has been remarkably free from natural enemies. Its apparent immunity, combined with its ability to thrive on soils too light and dry for most farm crops, has made it a favored species for planting in southern Lower Michigan. About twenty years ago, however, a pest appeared in the state which now threatens to make the planting of red pine unsafe.¹ This enemy is the European pine-shoot moth (*Rhyacionia buoliana* Schiff.), the larvae of which kill or deform young pine shoots.

OCCURRENCE AND HABITS OF THE MOTH

Known for a long time in Europe as a serious pest of pines, the European pine-shoot moth was first found in the United States in 1914, on Long Island. Evidently it had been introduced on nursery stock from Europe (1, 2). It is now known to occur over the eastern United States as far south as Virginia and west to Michigan and in southern Ontario (3). Apparently it was brought into Michigan on nursery stock from Illinois. The larvae attack many pines, but in North America they prefer red, mugho (*Pinus mugo*), and Scotch (*P. sylvestris*) pines (4, 5).

The adult moths fly during early summer and lay eggs near the tips of twigs, either on the twig itself or on a needle sheath, usually on the upper part of the tree. Young larvae, which are hatched in about ten days, bore into the bases of the needles through the sheath, killing the needles affected. Later in the summer they penetrate the buds and cause a flow of pitch, which hardens into a whitish mass. They overwinter in the bud or under the mass of pitch on the bud. When the trees begin to

* Paper from the Lake States Forest Experiment Station, maintained by the U. S. Department of Agriculture, Forest Service, in coöperation with the University of Minnesota, at University Farm, St. Paul, Minnesota.

¹ During the past decade two other insects have also become serious enemies of red pine in the Lake States. These are the red-headed pine sawfly (*Neodiprion lecontei* Fitch) and the Saratoga spittlebug (*Aphrophora saratogensis* (Fitch)).

grow the next spring, the larvae bore into the developing shoots, which curl slightly and die. A little later in the spring, they become full grown, pupate in the burrows, and, in about three weeks, emerge as adults (3).

Trees up to thirty feet tall or taller are attacked, but ordinarily red-pine stands which are not infested until the trees are over ten feet tall do not become badly injured. Control is possible by cutting off and burning infested tips in late spring or by spraying with arsenicals (3) or DDT. As a rule, neither method is practicable in any but very small plantations.

The moth has a tendency to infest and reinfest the same trees for several years in succession. For this reason it can develop into a serious menace in a small area in from three to five years. For the same reason, however, it does not, by its own power, extend into new areas very rapidly.

AREAS OF INFESTATION IN MICHIGAN

While no detailed survey has been made, a dozen foresters and entomologists² familiar with conditions in Lower Michigan have made observations on the occurrence of the moth. Although these observations vary in intensity and accuracy, combined they present the best available overall picture of the extent of infestation in the Lower Peninsula.

There is some evidence that the moth was introduced into Michigan in the vicinity of Ann Arbor in the early 1920's. It was first found only on ornamental stock, but about ten to fifteen years ago it began to appear in forest plantations. From this point, and possibly from other places to which shipments of infested nursery stock were made, it has spread over the greater part of the southern half of the Lower Peninsula. It is now found westward to Lake Michigan and north throughout the Thumb, and as far as Bay, Midland, Mecosta, and Muskegon counties. The heaviest infestations are reported from Washtenaw, Wayne, Monroe, Livingston, and Shiawassee counties. Moderately heavy infestations have been noted in Saginaw, Jackson, Hillsdale, St. Joseph, Cass, and Berrien counties, and parts of the Thumb. In most of the other counties south of the Bay City-Muskegon line light infestations have been observed.

Generally speaking, ornamental and highway plantings are often

² The author appreciates information furnished him by Dr. Samuel A. Graham, of the University of Michigan; Dr. E. I. McDaniel and Lester E. Bell, of Michigan State College; Paul E. Slabaugh, of the Soil Conservation Service; and the following foresters of the Michigan Conservation Department: R. L. Olmstead, R. G. Auble, A. H. Boelter, I. H. McFarland, L. O. Miller, R. E. Pfeifer, A. J. Phillips, and Paul Schroeder.

badly injured, especially where mugho pine has been included. Indications are that red pine is injured on poor sites more than on good ones. Within plantations insect attacks usually are spotty. In some places 75 per cent or more of the trees are damaged, whereas a short distance away all or most of the trees may be undamaged. Infestations usually do not appear until trees have become two to four feet tall. On small trees injury occurs largely in the tops; taller trees often have much of the infestation in side branches. Plantations bordering hardwood stands appear to be relatively free of the moth.

POSSIBLE AREAS OF INFESTATION

The natural range of red pine extended just into the northern part of the southern half of Lower Michigan, but the original stands were removed long ago. Over the years, however, numerous small plantations have been established in this area. As a rough estimate, perhaps 10,000 acres have been planted to it in the thirty-seven counties of the southern half. In this area there are about 66,000 acres of forest land in need of planting on which red pine would be the preferred species. There is also a considerable area suited for this species, which is now in cropland or pasture that should be planted to trees.

CONTROL OF THE MOTH

The following methods of control have been recommended by entomologists: (1) in the late spring cut off and destroy infested twig tips; (2) when the adults emerge apply a spray, made up of (a) three pounds of lead arsenate and one quart of fish oil in 100 gallons of water, and repeat it ten days later, or (b) three pounds 50-per cent wettable DDT, plus three pounds black leaf 155 in 100 gallons of water, or (c) miscible oil and DDT.

One landowner in the Thumb had some twenty acres of plantations which were hard hit by the moth. By picking off infested tips and spraying the trees with 2 per cent DDT powder, he kept damage to a minimum, but this method requires careful watching and a good deal of labor.

It is necessary to spray only the outer edges of individual trees or the borders of large plantations. Yet this method of control is too expensive for general use. Large blocks of plantations probably could be sprayed economically from airplanes or helicopters, but so far there are few such areas in southern Michigan.

Natural control may be more economical than spraying. Already heavily parasitized specimens of pine-shoot moth larvae have been found in Monroe County, and artificial release of parasites along with their natural spread might be quite effective. But the most effective natural control probably is cold winter weather, since the larvae die at temperatures of about -18° F.

THE CLIMATIC ZONE OF NATURAL CONTROL

To learn where cold weather capable of curtailing the spread of the moth occurs, an analysis of the weather records of the last two decades was made for seventy-five places in Lower Michigan, and the number of years in which there were temperatures of -18° F. or lower were plotted on a map (Fig. 1).³ Areas with similar numbers were grouped into five zones, which are listed below, together with the reasons for grouping them:

Zone 1. — Temperatures of -18° F. or colder occurred once or not at all. In this zone the insect can build up severe infestations and spread with little hindrance.

Zone 2. — Lethal temperatures occur one to three times, or, on the average, about every ten years. Severe infestations can be built up, but the spread of the insects will be more retarded than in Zone 1.

Zone 3. — Lethal temperatures come three to five times, or about every five years. Local infestations can become heavy, but there will not be much opportunity for their spread.

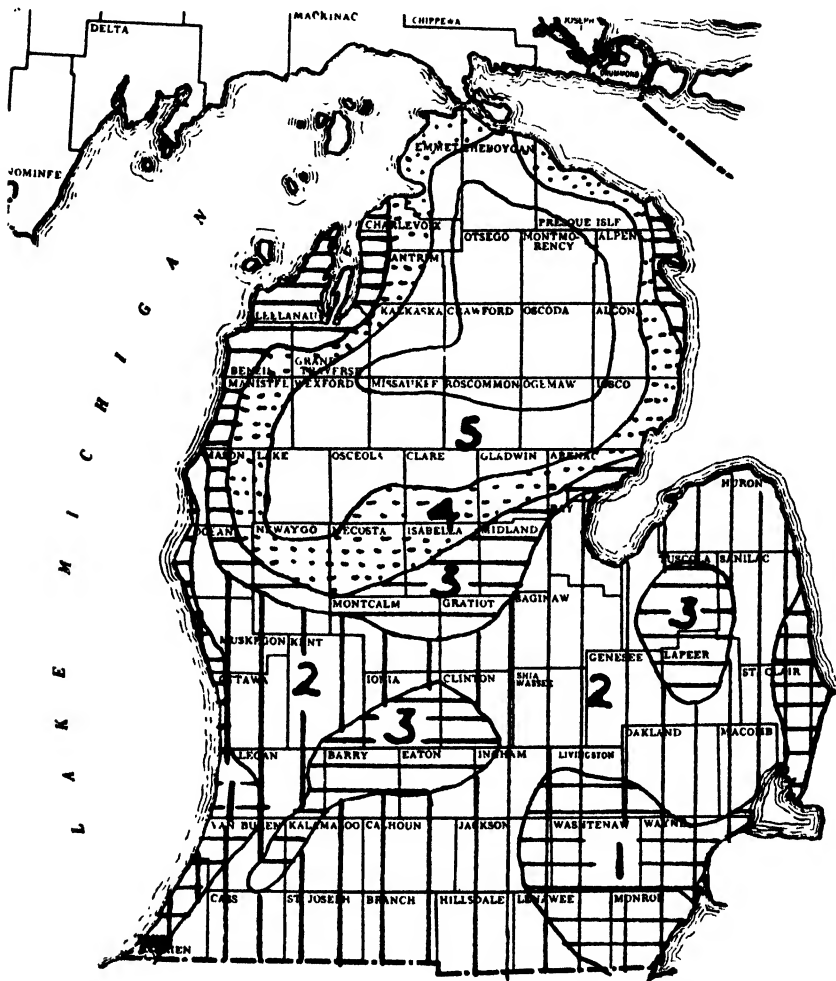
Zone 4. — About every three years, or five to ten times, there will be killing temperatures. Some local infestations may become relatively heavy, but there will be little opportunity for extensive serious attacks or for spread to new localities.

Zone 5. — Killing temperatures occur ten or more times, or every year or two. There is little opportunity for the insect even to establish itself.

If this reasoning is correct, severe damage from moths can be expected in red pine planted in southeastern Michigan within a narrow strip along the St. Clair River and the southern tip of Lake Huron, and within a nar-

³ Some weaknesses in this procedure are recognized: (1) the duration of the low temperatures is not known; (2) for most of the southern stations the lethal temperature occurred only once in the year recorded, but for others such temperatures occurred two or more times in the year; (3) temperatures at the point where larvae lived may have been either higher or lower than those recorded at weather stations. However, these data are the best available and, despite their drawbacks, are useful.

row strip along Lake Michigan from about Ludington to the Indiana border (Zone 1 in Figure 1). Throughout most of the rest of the southern



ZONE SYMBOLS AND NO. OF OCCURRENCES
OF -18°F. OR COLDER IN 20 YEARS






1		0-2	3		3-5
2		2-3	4		5-10
5		10-15 & 15-19			

FIGURE 1

half of Lower Michigan (Zone 2) red pine may eventually become heavily damaged. Individual infestations may become severe, but their spread is apt to be highly restricted in portions of Lapeer and Tuscola counties; portions of Clinton, Ionia, Kent, Eaton, Barry, Allegan, Kalamazoo, and Van Buren counties; and in a belt including parts of Arenac, Bay, Midland, Isabella, Mecosta, Gratiot, Montcalm, and Newaygo counties, and extending north to the Lake Michigan shore and up to Charlevoix, and along the Lake Huron shore in Alcona, Alpena, and Presque Isle counties (Zone 3). Throughout the rest of the northern half of the Lower Peninsula the moth either is not likely to establish itself or is not apt to cause serious damage (Zones 4 and 5). For many purposes Zones 1 and 2 could well be combined.

CONTROL MEASURES PROPOSED

In view of the facts now known certain recommendations can be made to minimize the damage from the European pine-shoot moth in Lower Michigan. Some of them are as follows:

1. New red-pine plantations should not be established adjacent to plantings infested with the moth.

2. Present infestations should be controlled wherever additional plantings are contemplated. Special efforts should be made in the western part of the state, where the moth does not yet appear abundant and where rather extensive red-pine plantations already exist.

3. In the eastern tongue of Zone 1, where the infestation is most severe, suitable races of the more resistant ponderosa and Austrian pines should be sought as substitutes for red pine.

4. Red pine should not be planted on poor sites.

5. The use of mugho pine should be discouraged wherever red- or Scotch-pine plantations are to be established.

6. Unless constant vigilance is exercised and controls are applied at the first sign of infestation, red pine should not be planted in the southern half of Lower Michigan, except in Zone 3. Even here some damage is likely to occur if no artificial control is used.

7. From a long-range point of view red pine trees apparently resistant to damage from the moth should be utilized as a source of seed or breeding material for developing resistant planting stock.

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"Pusilla res mundus est nisi in illo
quod quaerat omnis mundus habeat."
— SENECA, *Naturales Quaestiones*

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BOTANY

SEASONAL ASPECTS OF THE BERMUDA ALGAL FLORA*

ALBERT J. BERNATOWICZ

FLORISTIC studies of the algae of Bermuda have been published by Collins and Hervey (1917) and by Howe (1918). The work of Collins and Hervey is especially useful, since it is based on their own extensive collections over a period of six years and on the smaller collections of earlier authors. Howe made no attempt to report a complete list of species, but he furnished interesting and valuable descriptive remarks on some of the more common species. Although these authors mention that certain species have "their seasons," they give no indication of the extent of the seasonal changes which occur. Field observations by the writer from February to mid-September, 1949, disclosed the seasonal variations of the algal flora to be sufficient to affect the aspects of some areas.

Considerable changes in the algal flora take place notwithstanding the uniform and mild climate. The temperature range covers only about eleven degrees centigrade. Air temperatures in February and March average from 18.5° to 21.5° C.; in May and June they fluctuate from 23.5° to 25.5° C., and August brings the warmest days of the year, with temperatures about 29.5° C. The sea is generally one to three degrees cooler than the air. The mean tide range is about 2.4 feet, and the mean spring range is about 3 feet.

At all seasons in calm areas a short fuzz of several more or less generally distributed species covered the rocks between tide marks. *Bostrychia tenella* (Vahl) J. Ag. and *Polysiphonia Howeii* Hollenberg persisted about high-water mark practically everywhere. There were none of the large intertidal forms such as are found on northern shores. Whatever seasonal changes may have taken place above low-tide level did not appreciably alter the aspects of the communities there.

The communities in three types of habitat near and below low-tide level were studied frequently between late winter and early autumn. The first of these habitat types, a landlocked salt-water pool or fishpond, is

*Contribution from the Department of Botany, University of Michigan, No. 924, and from the Bermuda Biological Station for Research, No. 162.

extremely well shaded and protected from wave action. The largest of these pools is only ten feet in diameter and six feet deep at low tide. They are often more nearly six feet in diameter and two feet deep. Steep rock sides surround these pools, but there is always tidal access, either through small openings in the walls or through underground connections with the sea. As a rule, the ponds are heavily shaded by trees or ledges. The bottoms are commonly of soft mud over coquina.

These pools displayed a richer flora during February and March than did any other habitat. *Bryopsis plumosa* (Huds.) C. Ag., *B. hypnoides* Lamx., *Monostroma latissimum* (Kütz.) Wittr., and *Halymenia bermudensis* Collins and Howe were the most conspicuous species. Toward the end of March *Ulva Lactuca* L. also became prominent. *Caulerpa racemosa* (Forssk.) J. Ag., *C. crassifolia* (C. Ag.) J. Ag., and *C. sertularioides* (Gmel.) Howe were present but less obvious. *Caulerpa racemosa* is of particular interest because it was the only species also common in the two other habitats to be described. These few species steadily increased in quantity, so that in April the pool vegetation was luxuriant, with no one species dominant.

The luxuriance was even more pronounced by late spring or early summer, when *Bryopsis* choked the pools. *Ulva* and the species of *Caulerpa* were still important members of the community. *Monostroma* and *Halymenia* were fading, and disappeared in June. No new important species were recognized. In contrast, the late summer and early fall vegetation of August and September in the pools was sparse, being dominated by tufts of *Myxophyceae*. *Bryopsis* was scanty or lacking, and the blade-like *Monostroma*, *Ulva*, and *Halymenia* species were altogether absent. Although *Caulerpa crassifolia* and *C. sertularioides* were still rather abundant, *C. racemosa* persisted only in the most shaded niches.

The general impressions obtained from small, easily scanned pools are more likely to be accurate than those formed from viewing the next type of habitat to be discussed, which may be called "Thalassia-cove type." Such a sunny, calm cove is typically 150 to 300 feet long and about as wide. The water is usually shallow enough to permit wading, and the bottom is covered with beds of the turtle grass *Thalassia testudinum* Konig and Sims. A mangrove thicket (*Rhizophora Mangle* L.) is commonly found at the head of the cove. The button bush, *Conocarpus erecta* L., and the black mangrove, *Avicennia nitida* Jacq., line the smooth coquina sides. A narrow shelf of rock extends a few feet from the sides of the cove and then drops several inches to a bottom of gritty,

calcareous mud, which smells of hydrogen sulfide. Little wave action disturbs the waters. The mangrove thicket and its dominant algal component, the *Bostrychia* complex, belong to a distinctive ecosystem, which will not be considered at this time.

The flora of such a cove in February and March was particularly monotonous. The dominant alga was a *Sargassum*, the leaves of which were covered with silt and detritus. Second in abundance were two of the Rhodophyceae, *Amphiroa fragilissima* (L.) Lamx. and *Spyridia filamentosa* (Wulf.) Harvey. *Spyridia*, afloat or attached near the shore, was of an unsightly buff color. The *Amphiroa* had the same bleached color, but grew on the bottom as a cover through which blades of *Thalassia* protruded. Two species of Phaeophyceae, *Scytosiphon Lomentaria* (Lyngbye) C. Ag. and *Aegira Zosteræ* (Mohr) Fries, were prominent in February. *Scytosiphon* was restricted to areas covered by only a few inches of water at low tide, while the stands of *Aegira* extended to a depth of three feet or more. The two species soon became scarcer and they were absent in April. The genera *Sargassum*, *Spyridia*, *Amphiroa*, *Scytosiphon*, and *Aegira* may be said to be responsible for the drab appearance of these coves in winter and early spring. In addition, a myxophycean scum of *Lyngbya majuscula* Gom. was present in some areas and locally changed the appearance. The Chlorophyceae were represented mainly by a few epiphytized calcareous members of the Codiaceae and by *Cymopolia barbata* (L.) Lamx. *Caulerpa racemosa* existed in small quantity and did not develop as rapidly here as it did in fishponds.

During late spring and the beginning of summer there seemed to have been very little noticeable change. This superficial similarity was due largely to the continuing dominance of the drab *Sargassum*, *Spyridia*, and *Amphiroa*. *Scytosiphon* and *Aegira* were lacking, however; the phaeophycean genera were now *Padina* and *Dictyota*. Moreover, the number of *Cymopolia* and *Caulerpa* had increased. Clean young green plants of the Codiaceae, including *Halimeda Monile* (Ell. and Sol.) Lamx., *H. tridens* (Ell. and Sol.) Lamx., *Udotea Flabellum* (Ell. and Sol.) Howe, *Penicillus capitatus* Lamk., and *Avrainvillea* sp., were present in the beds of *Thalassia*. At this time the scum of *Lyngbya* was supplemented by increasingly frequent gelatinous tufts of *Symploca hydroides* Gom. A new red alga, *Acanthophora spicifera* (Vahl) Børg., arose and quickly became conspicuous during this season. During the transition from spring to summer, then, new species of Phaeophyceae began to appear; among the Chlorophyceae the change was more in numbers of thalli than

in species. The Rhodophyceae and the Myxophyceae changed relatively little either in species or in numbers during the same period.

Although the aspects of the earlier seasons were determined mainly by the drabness of Sargassum, Spyridia, and Amphiroa, the late-summer appearance of the quiet coves depended upon an abundance of calcareous forms and Myxophyceae. The most important change in August was probably the disappearance of Spyridia from near the surface, with consequent exposure of the steadily increasing Codiaceae and Dasycladaceae. Of these families, Halimeda, Penicillus, Udotea, Cymopolia, *Neomeris annulata* Dickie, and *Acetabularia crenulata* Lamx. are calcified, and at this season they flourished. In particular, *Acetabularia* made a field of tiny parasols, which during low tide was barely immersed in some parts of the coves. Among the Phaeophyceae a calcareous species of *Padina* was as abundant as it had been in June and added to the general impression that the flora was largely of calcareous algae. Coincident with this dominance of calcareous green and brown algae there was a decrease of the calcareous red alga *Amphiroa*. The general increase among calcareous forms was accompanied by an increase of the two blue-green species, *Lyngbya majuscula* and *Symploca hydroides*. Growing at the surface of the water, here and there they obscured the bottom dwellers.

In summarizing the seasonal aspects of the calm and sunny *Thalassia* coves we note that the monotonous colorless flora of winter became more interesting in late spring because of the arrival of two new brown algae and the increase of green calcareous forms. The calcareous forms continued to increase until they dominated the bottom in late summer, when they were locally hidden by blue-green algae of the surface waters.

The third type of habitat consists of surf-swept rocky shores. Although characterized by somewhat more active waters than are the previous areas, the situation is not one of heavy wave action. The shore is of coquina, eroded into a mass of knife edges. It rises abruptly from the water, sometimes in clifflike proportions. The continuous algal fuzz of calmer shores is largely lacking, possibly because of the scouring action of the surf. Occasional small and shallow rock pools dot the shore. The rock bottom is interrupted at frequent intervals by patches of sand and coral heads. The slope of the bottom is steeper than that of mud bottoms; nevertheless, within fifty feet of the shore it is probably no more than ten feet below low-tide level.

A characteristic feature of such shores in February and March was the abundance of small things. There was a wealth of species, but the

plants were poorly developed, and few of the species grew in great quantity. Sargassum, scrubby at low-tide level but larger in deeper water, was dominant. Of the several other Phaeophyceae to be found only *Dictyopteris Justii* Lamx. and *Colpomenia sinuosa* (Roth) Derbes and Solier were conspicuous, although neither was at full size. Several species of Dictyota appeared in March. Among the green algae the ubiquitous *Caulerpa racemosa*, still small, was more frequent here than in either of the previous locales at the same season. *Codium intertextum* Collins and Hervey, a prostrate species, was rare in February but became abundant in March. During March a few rhodophycean species were sufficiently evident to make these shores much more colorful than were the quiet coves. These red algae included *Dasya* sp., *Laurencia* sp., *Lophocladia trichoclados* (Mertens) Schmitz, *Dudresnaya crassa* Howe, *Trichogloea Herveyi* Setchell, and several species of Liagora.

Many of the small plants never became large or abundant enough to affect the overall appearance, but some were rapid growers and flourished by late spring. *Caulerpa racemosa*, for example, grew to full size and luxuriance in May. *Codium intertextum* retained its early prominence. Colpomenia reached a magnificent maximum early in May and was fading in June. Indeed, it and the other Phaeophyceae dominated the scene during May and June. Sargassum, Dictyopteris, and *Zonaria zonalis* (Lamx.) Howe did so by virtue of their relatively great size while *Pocockiella variegata* (Lamx.) Papenf. stood out by its great abundance. The red algae, on the other hand, almost disappeared. Of the earlier inhabitants only Lophocladia remained abundant, and a single new arrival, *Laurencia obtusa* (Huds.) Lamx., added a little variety.

In late summer the changes were again very pronounced. *Caulerpa racemosa* and *Codium intertextum*, though still present in quantity, seemed past their maxima in both numbers and vigor. The brown algae were still dominant but were obviously waning. For example, Dictyopteris had reached its largest size, but the plants were battered and epiphytized. Pocockiella, still plentiful, was not so generally distributed as before, which seemed to indicate that some of the colonies had died out. And the great masses of Colpomenia were quite gone. The Rhodophyceae fared worst of all, for not a single species was seen in quantity sufficient to make a mark on the overall aspect. Instead, frequent gelatinous tufts of Myxophyceae floated from the remnants of larger algae and somehow added to the impression of a moribund flora.

We may summarize the aspects of surf-swept rocky shores as charac-

terized in the early spring by numerous small, perhaps young, plants. The red algae for the most part showed only a brief period of abundance; the brown algae grew rapidly and persisted to dominate the summer scene, showing signs of diminishing only in August or September. As in both the calmer habitats, Myxophyceae were important members of the community in late summer. Furthermore, *Caulerpa racemosa* appeared in quantity earlier and persisted later here than in either of the quiet areas. In each situation it was a rock *Caulerpa* under consideration, but no attempt has been made to compare the several varieties and forms of *Caulerpa racemosa* from each habitat.

A logical extension of these descriptions of habitats and aspects would include the most active waters, that is, the outer reef areas. Unfortunately, these rough waters did not permit enough observations to furnish a report.

The writer wishes to express his thanks to Professor Wm. Randolph Taylor, of the University of Michigan, for his guidance and for the opportunity to undertake these studies as his research assistant. Through the kindness and coöperation of Professor Dugald E. S. Brown, formerly director of the Bermuda Biological Station, the author was provided with the necessary facilities.

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PERMANENT MOUNTS OF AGAR PLATES OF STREPTOMYCES FOR USE AS HERBARIUM SPECIMENS*

KENNETH LESTER JONES

MANY authors in describing species of *Streptomyces* have given little or no information on the characteristics of colonies on agar or gelatin plates. Consequently, in the latest edition of *Bergey's Manual*¹ colonies are not even mentioned in the descriptions of thirty-five of the seventy-three recognized species. Organisms as well known as *Streptomyces griseus* and *S. lavendulae* do not have colony descriptions.

I believe that colonies of *Streptomyces* possess convenient macroscopic characteristics of taxonomic validity that are not duplicated in larger and less definite growths on slopes and plates. These include size, shape, nature of the margin, topography, position of the aerial mycelium, color of the colony and of the surrounding medium, and tendency to produce sectors.

Colonies must be grown in a standard manner to give significant data for analysis and comparisons. This requires: (1) the use of organisms freshly isolated from natural substrata, or at least vigorous organisms of known cultural history; (2) media of known chemical composition; (3) a set plan of inoculation (Pl. I); and (4) constant physical conditions.

Anyone who has cultured only bacterial colonies has a surprise in store for himself when he first grows *Streptomyces*. Given conditions for full development, some species produce elaborate colonies. For example, I have one species, especially interesting because it is from Bikini, in which the aerial growth takes on a pattern of green, brown, flesh-colored, and white areas against a brilliant orange vegetative base. One has been observed in which the colony is hollow with a central pore, exposing coralloid growths lining the interior. Another develops a leathery stroma which cracks into concentric platelets that are thrust upward on edge.

*Paper from the Department of Botany, University of Michigan, No. 920. Financial aid was given by Horace H. Rackham Faculty Research Grant No. 703.

¹Bergey, D. H., and Others, *Bergey's Manual of Determinative Bacteriology*, Sixth Edition, xvi + 1529. Baltimore: Williams and Wilkins Co., 1948.

Quantitative characteristics, including the frequency of sectors, may be analyzed statistically when hundreds or thousands of colonies of a given isolate are grown in a standard manner. In such colonies size, for example, is an index of growth rate and of the chemical and physical relationships between colonies. Relatively few isolates, in my experience, have a strong tendency to sector or to exhibit a wide range of fluctuating variations.

Although taxonomic works do not at the present time make it possible to take advantage of the rich criteria that colonies of *Streptomyces* afford for the identification of species, nonetheless these criteria are useful in other ways, for example, in the preliminary sorting of isolates from a given soil and in comparing those of one soil with another to get some idea of natural distribution.

Fortunately, permanent preparations of the agar plates containing the colonies can readily be made as follows: A 1 : 1,000 dilution of HgCl_2 is carefully poured on the agar plates and left there for a half hour. The entire agar plate is then lifted as a thin disk from a petri dish with the aid of a spatula and is placed intact on filter paper. I use a size of paper sufficient to accommodate four agar plates with their labels. A few sheets of filter paper are placed on the agar and the process is repeated until about six layers of specimens are in the pile. A slight weight such as a magazine or two is placed on them, and the material is left to air-dry at room temperature. The filter paper is changed after two days to facilitate drying and to prevent the agar from adhering to the paper. When thoroughly dry, the agar plates are cellophane-like films that retain their colors remarkably well. The films are placed in transparent envelopes and filed in drawers or mounted on standard herbarium sheets (Pl. I).

A few words of caution may be helpful. The original layer of agar medium should be fairly thick, say, 3 mm., and of a 2 per cent agar content. A thinner plating or a more dilute agar will result in the disk breaking or folding when it is lifted from the petri dish. The other extreme is apt to be equally unsatisfactory since the vegetative stroma of a colony may contract at the time of sporulation and crack heavy agar into irregular chunks. If the bath of bichloride is left on the agar too long, the physical composition of the gel is affected, so that the dry films crumble to powder when handled. Treatment with the bichloride kills the *Streptomyces*, which is a necessary precautionary measure, but it also permanently protects the agar against any possible microbial contamination,

which here would be rapid and ruinous. Fungicides or killing agents containing alcohol darken most of the colonies instantaneously.

Sometimes excellent specimens are obtained when agar disks are directly exposed to the air on a suitable flat surface, without weighting them down with absorbent papers. Unfortunately, the films are apt to curl as they dry, for the margins pull away from the underlying paper. Too heavy a weight on stacks of drying plates flattens the colonies unduly and causes the agar to stick to the paper. The same degree of care must be exercised in handling the dried agar films that is required in working with herbarium specimens of flowering plants, since both are crisp and will crumble if maltreated. A relatively few isolates bear their spores so loosely that they are mostly lost when the bichloride solution is applied or in the subsequent contact with paper. I have not solved this difficulty, but I believe that a film of quick-drying adhesive, applied before flooding the plate, might prove satisfactory.

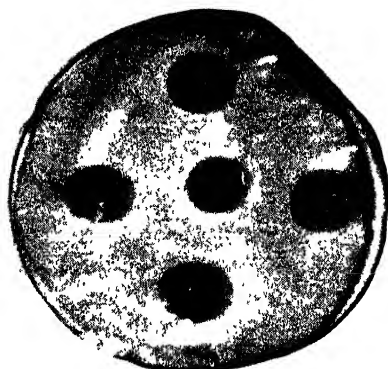
The dried specimens admittedly do not show the form and structure of the colonies as well as do the fresh cultures because a flattening and shrinking occur. They make it possible, however, to assemble and compare thousands of isolates at one time, which is entirely out of the question with living cultures. It is also important to have permanent records of actual material of organisms freshly isolated from nature, where, as in *Streptomyces*, variation is a major problem and many isolates do not survive laboratory conditions.

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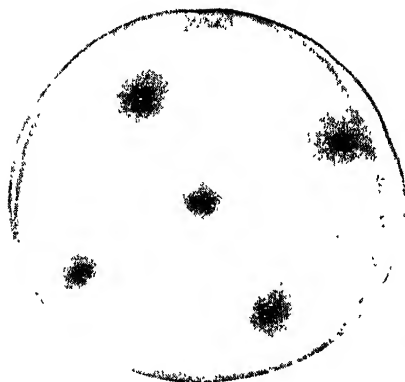
PLATE I



1



2



3



4

Permanent dried and sterilized agar plates of *Streptomyces* isolates from soil: (1) Number IV-40 on Bennett's medium, (2) Number I-97 on Czapek's medium; (3) Number I-5 on Czapek's medium, and (4) Number I-18 on Bennett's medium

THE DEVELOPMENT OF THE YOUNG VEGETATIVE MYCELIUM IN STREPTOMYCES*

KENNETH LESTER JONES

NO ONE, so far as I am aware, has given special attention to the development of the young vegetative mycelium of *Streptomyces*. Several investigators, including Waksman (1919), Drechsler (1919*a-b*), Lieske (1921), Carvajal (1947), and Klieneberger-Nobel (1947) have briefly commented on the subject or presented illustrations. McClung (1949) has studied intensively many species of the allied genus *Nocardia* (*Proactinomyces*).

In the present work spores or aerial hyphae of *Streptomyces* were germinated and studied on glycerol nutrient agar blocks according to the method of Jones (1940) as improved by McClung (1949). After twelve hours of incubation at 22° C. the mounts were first observed microscopically. Most isolated spores and fragments of filaments do not germinate, as McClung (1949) found true of *Nocardia* filaments. Camera lucida drawings were made under a 4-mm. objective at intervals of one to two hours of growing material, which was kept at 22° C. in moist chambers when not under observation.

The text figures for this paper have been selected from several dozen studies to illustrate the main findings. Generally, spores of *Streptomyces* germinate at two opposite positions at different times (Figs. 10*a-b*), and hence the germ tubes are unequal (Fig. 1*a*). Short aerial hyphae that occur in the suspensions with the spores may also grow at both ends (Fig. 4), as McClung (1949) illustrated for *Nocardia*, which is asporous. Usually a primary filament curves near each end, so that the direction of the tips is reversed (Figs. 1*d* and 11*c*), or it produces one or more sharp curves centrally (Figs. 6, 7, and 10).

The curved ends may grow alongside the median portion of the main hypha or its branches (Figs. 2-3). Laterals may change their original course and become parallel to and even press against the primary filament

*Paper from the Department of Botany, University of Michigan, No. 921. Financial aid was given by Horace H. Rackham Faculty Research Grant No. 703.

(Figs. 4*d* and 5) or against one another. They grow toward one another as though mutually attracted by a stimulus and, once aligned, they do not cross but continue to elongate, whether headed in the same or opposite directions. This phenomenon may occur between filaments of separate colonies that happen to be proximate. Fascicles of as many as six strands have been seen in growths older than those illustrated in this paper. This kind of organization, incidentally, is found in the coralloid aerial growths visible macroscopically on some colonies; for an example see Lieske (1921), p. 79. The affinity of hyphae also calls to mind the belief of Klieneberger-Nobel (1947) that there is a fusion of filaments in the primary mycelium to form initial cells "which consist of darkly staining nuclear bodies surrounded by cytoplasm and later enclosed by a cell wall." The initial cells are supposed to produce the diploid aerial mycelium.

The curved median portion of a primary filament serves as a center for the development of hyphae that will radiate outwardly to form very early a symmetrical growth, circular in outline. Such an individual is almost from its inception veritably an "actinomycete" or ray fungus. Figure 10 shows this happening from a sigmoid curved portion, and Figure 7 represents it from a region that is bent into a circle.

Thus, in the material that I have studied, the initial filament usually loses its position of dominance very early (Figures 4 and 5 show exceptions). Lieske's illustrations (1921, pp. 53 and 62) agree. McClung (1949) found that in the closely related species of *Nocardia* which have persistent mycelia the initial filament commonly remains dominant for a much longer time.

If a spore has only one germ tube (Fig. 9), the primary hypha may become contorted and stunted, but the laterals may be vigorous and overgrow one another and thus form a complex network. Drechsler (1919*b*) illustrated such germ tubes and also spores with two and three tubes, as did Carvajal (1947) in his interesting photographs of submerged growths.

The present investigation is exploratory. Its findings so far do not offer much encouragement to the taxonomist since the results from a single strain are so variable in some instances (Figs. 4–8). I believe, however, that more organisms must be studied before the characteristics of young vegetative mycelia can be relegated to the long list of invalid ones for this enormous and difficult genus. Drechsler (1919*a*), who was hopeful of establishing specific characteristics, stated: "From 1 to 4 germ tubes are then produced, apparently more or less successfully, the ap-

proximate number being, in a measure, characteristic of the species. Specific characteristics are expressed also in the diameter of the hyphae, and in the frequency of branching." McClung (1949) did not find specific differences between species of *Nocardia* that form an extensive mycelia and are most like *Streptomyces*. Whatever its taxonomic implications, I believe that developmental studies of the young vegetative mycelium will elucidate our ideas on growth, morphogenesis, and nutrition in a genus of considerable practical importance to man.

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NOTE

All the drawings were made with the aid of a camera lucida by means of a 4-mm. objective and a 12.5 ocular, and all are to the same scale. The bar scale on each figure represents ten microns. The material grew on glycerol nutrient agar blocks and was kept at about 22°C., except as otherwise stated.

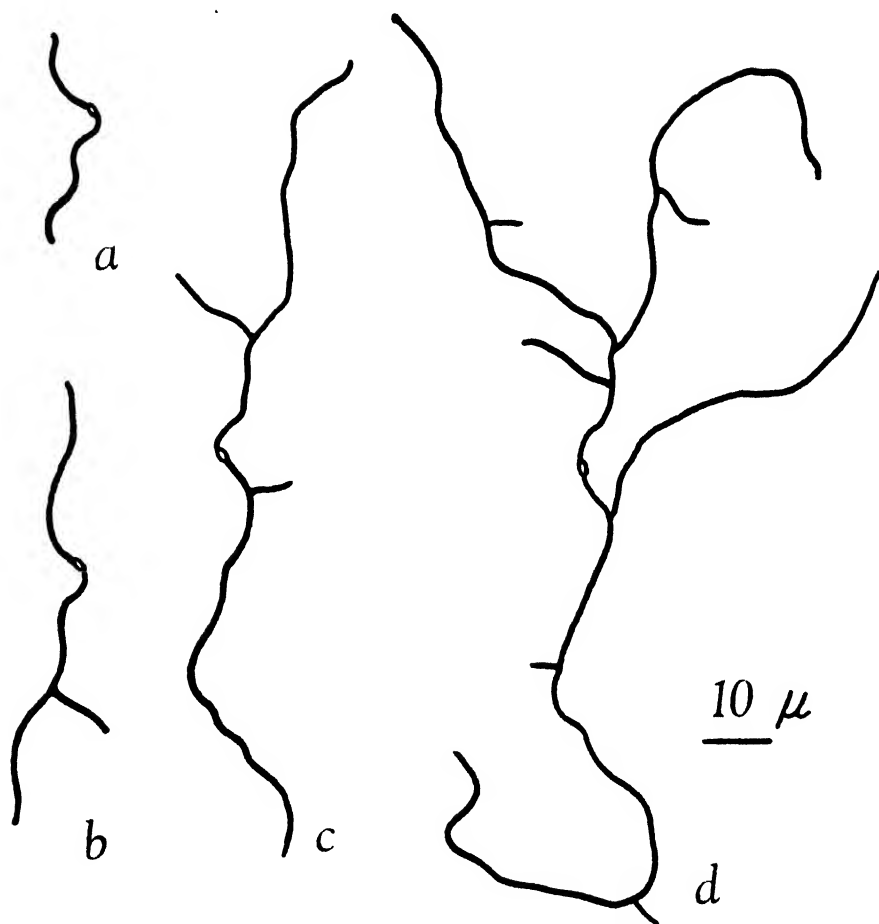


FIG. 1. Unidentified species 1-Sch.: *a*, 9 hours after inoculation; *b*, 13 hours; *c*, 17 hours; *d*, 22 hours

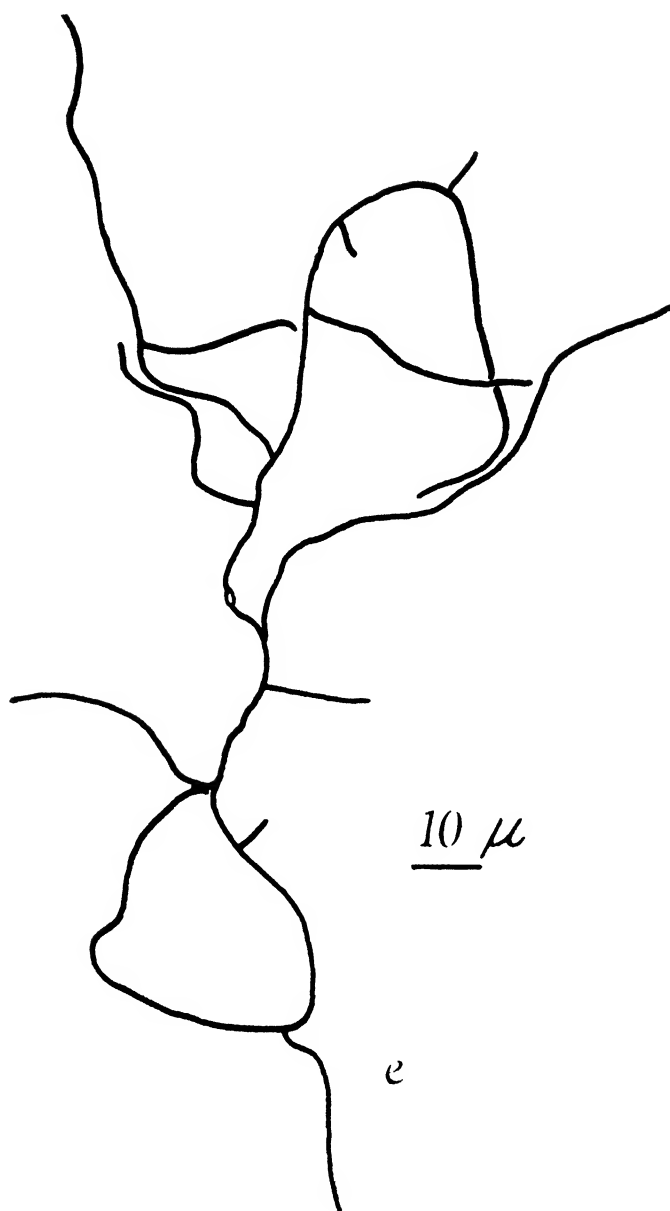


FIG. 2. 1-Sch. (*continued*): *e* is the same as *d* of Figure 1, after having been kept twelve hours longer at a temperature of 15° C.

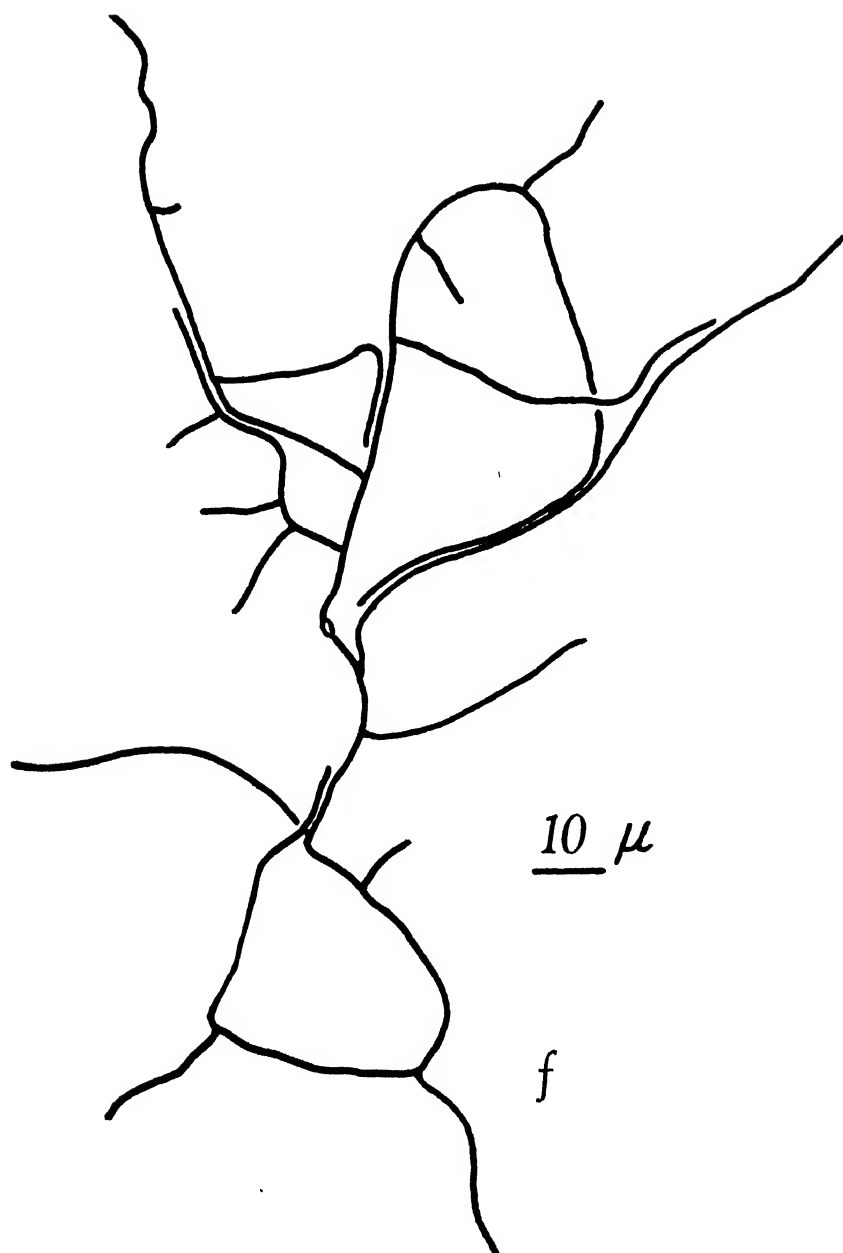


FIG. 3. 1-Sch. (*continued*): *f* is the same as Figure 3, after having been kept five hours longer

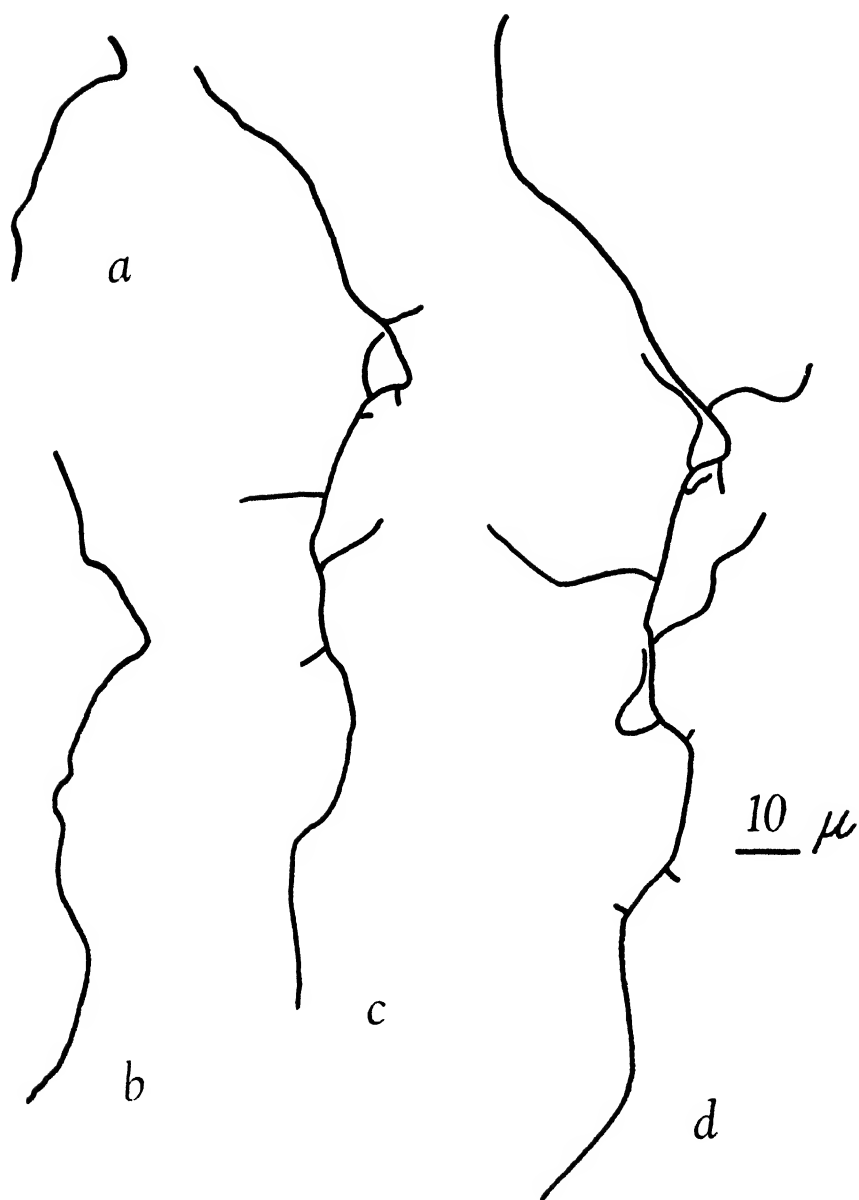


FIG. 4. Unidentified species 21-11, Study A: *a*, 27 hours after inoculation; *b*, 30 hours; *c*, 32 hours; *d*, 33 hours

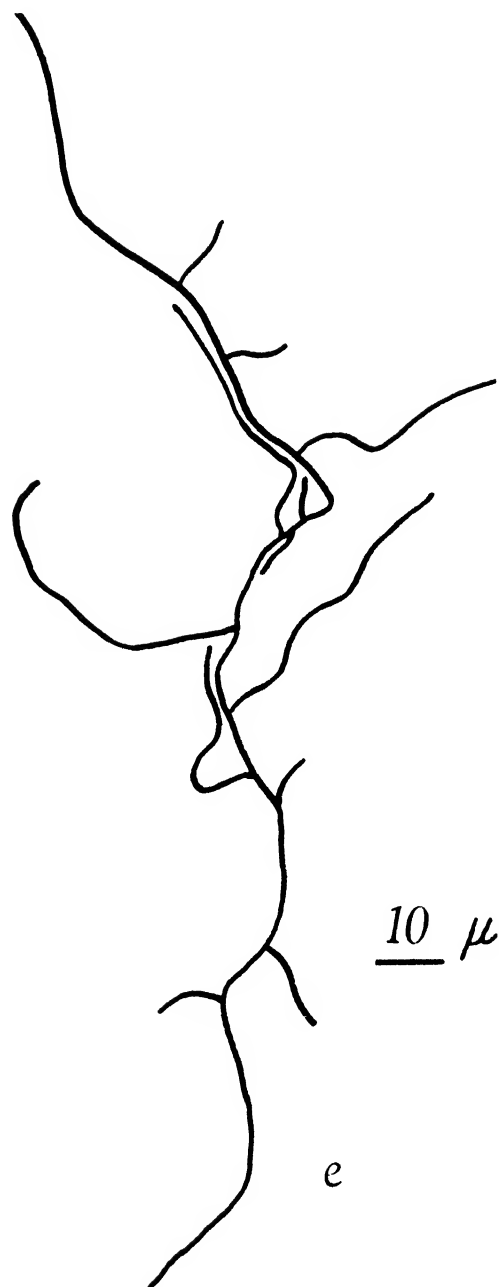


FIG. 5. Unidentified species 21-11, Study A (*continued*)
e, 34 hours after inoculation

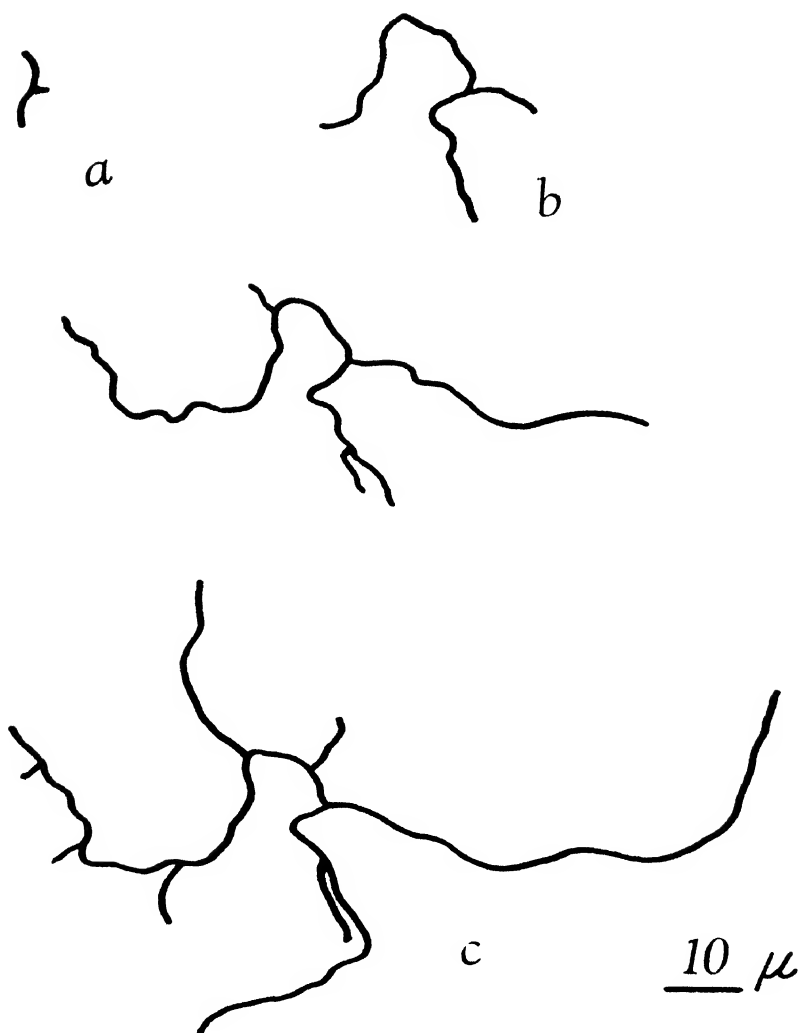


FIG. 6. Unidentified species 21-11, Study B: *a*, 20 hours after inoculation; *b*, 22 hours; *c*, 30 hours

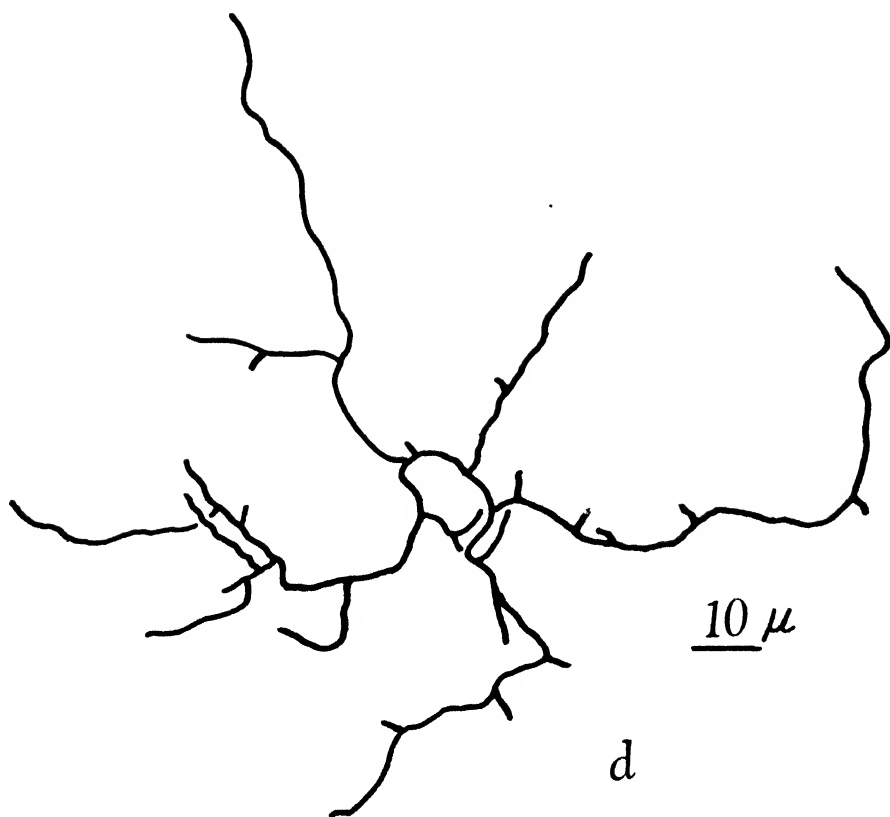


FIG. 7. Unidentified species 21-11, Study B (*continued*):
d, 55 hours after inoculation

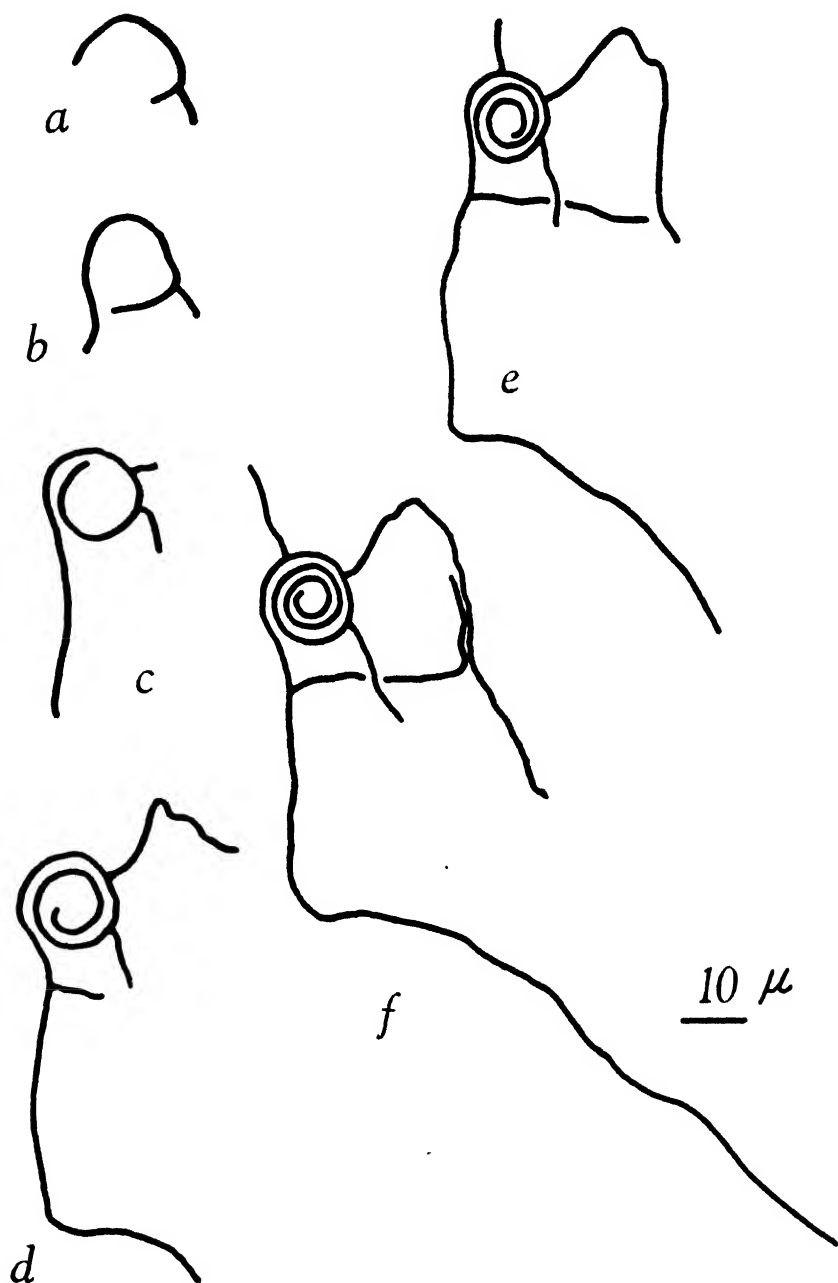


FIG. 8. Unidentified species 21-11, Study C: *a*, 27 hours after inoculation; *b*, 28 hours; *c*, 30 hours; *d*, 32 hours; *e*, 33 hours; *f*, 34 hours

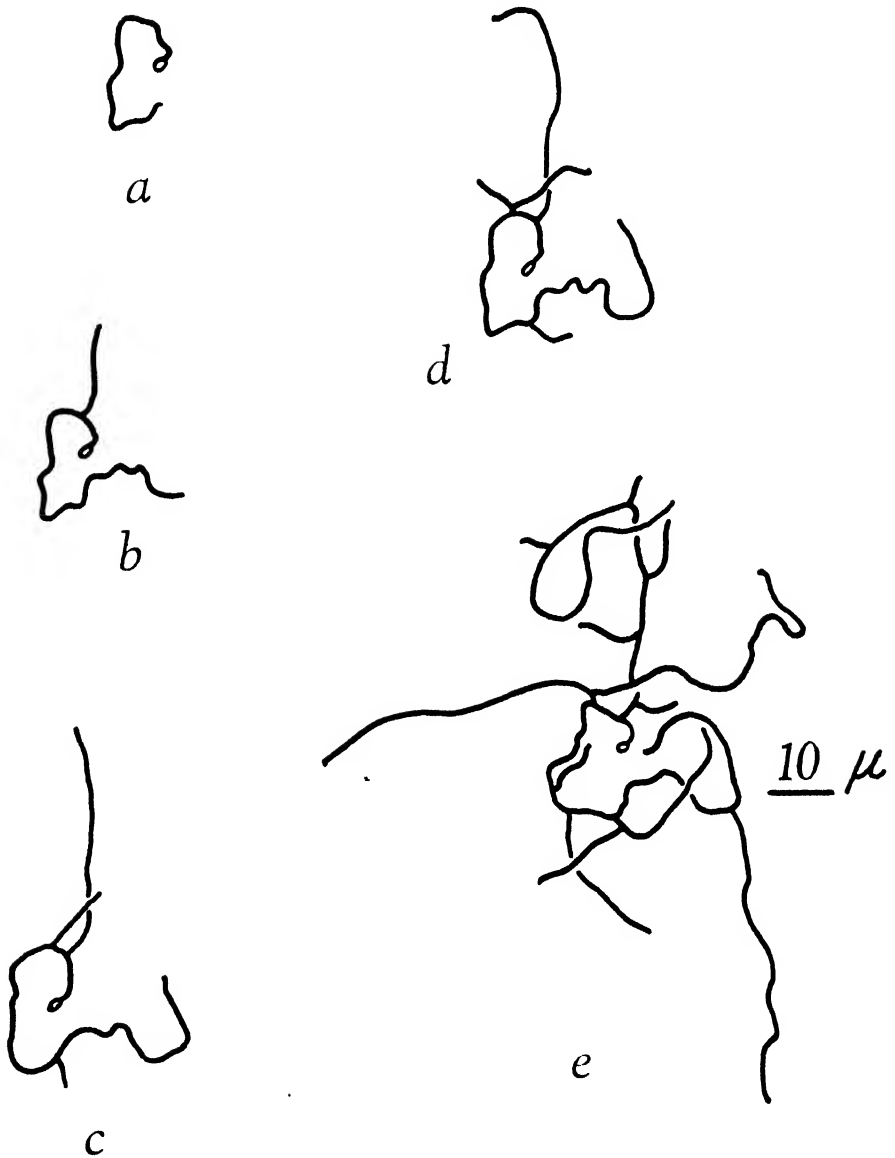


FIG. 9. Unidentified species 21-3: *a*, 21 hours after inoculation; *b*, 25 hours; *c*, 31 hours; *d*, 33 hours; *e*, 41 hours

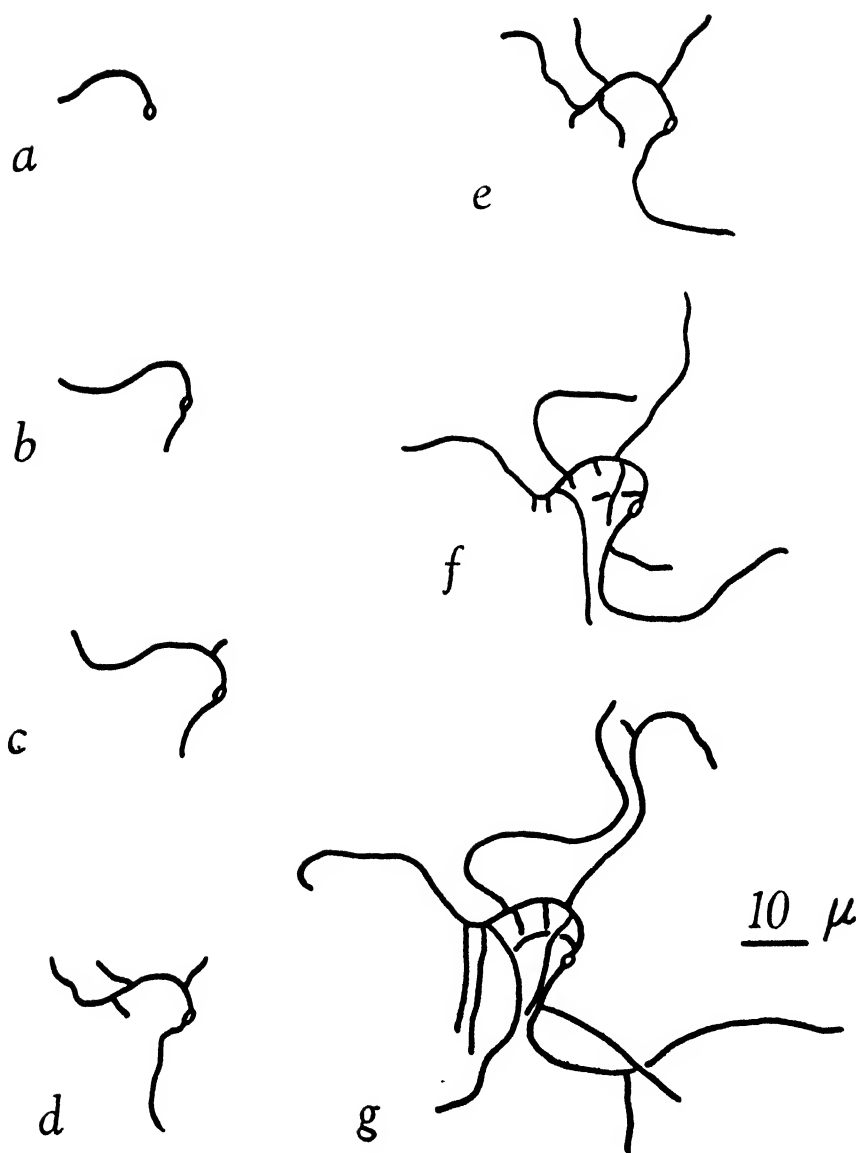


FIG. 10. *Streptomyces griseus*: a, 23 hours after inoculation; b, 26 hours; c, 27 hours; d, 30 hours; e, 33 hours; f, 37 hours; g, 44 hours

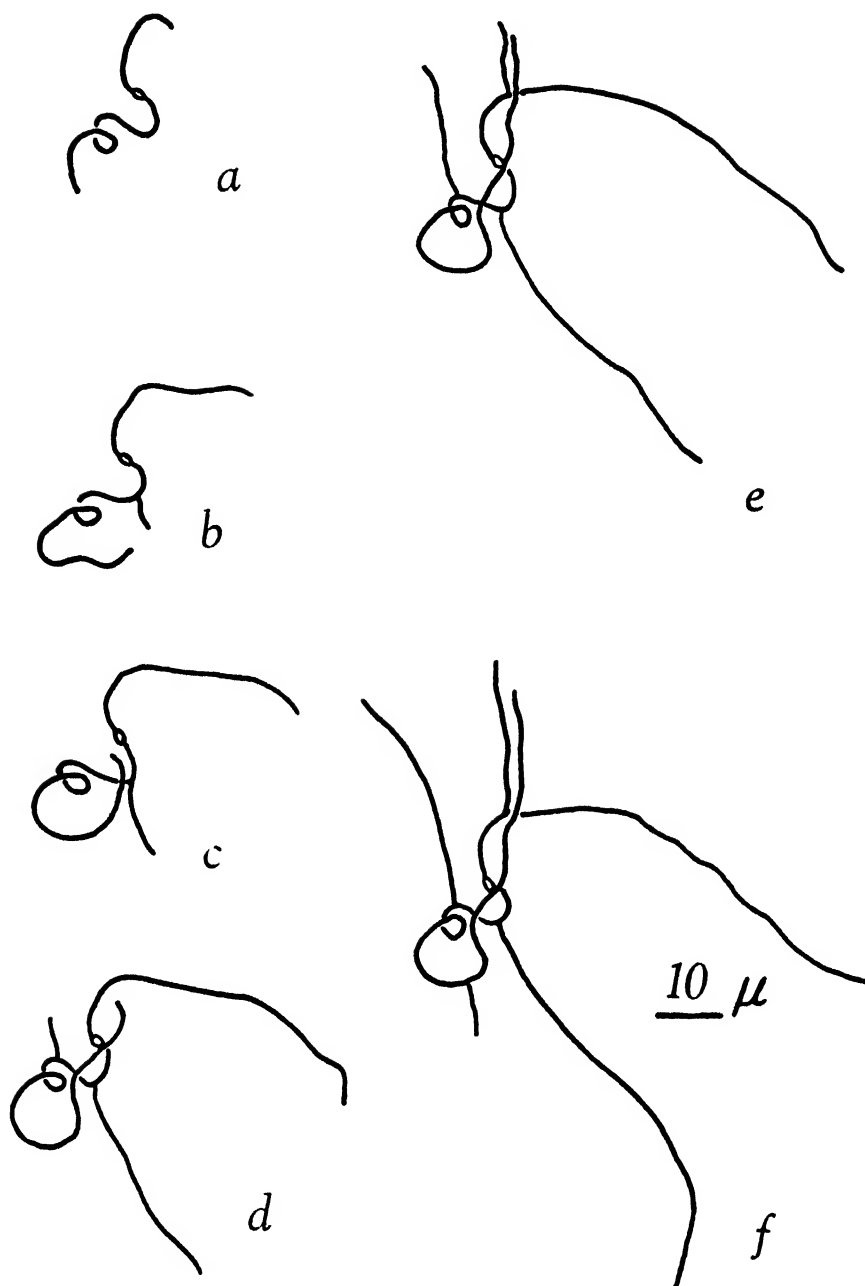


FIG. 11. *Streptomyces lavendulae*: a, 18 hours after inoculation; b, 20 hours; c, 21 hours; d, 22 hours; e, 23 hours; f, 24 hours

INHERITANCE IN *CUCURBITA PEPO**

EDWIN B. MAINS

CUCURBITA PEPO includes certain of the squashes, pumpkins, and gourds. During the war, when the writer was responsible for courses in applied botany and genetics at the University of Michigan, squashes and gourds were used for class purposes, and the selfs and crosses produced certain characters which have been studied for inheritance.

YELLOW SEEDLING

In the progeny of a self derived from a cross between varieties of summer squash, seedlings occurred which lacked chlorophyll. These were light yellow and died within two or three weeks. The character appears to be similar to that known as luteus in maize. In the progeny of the self there were 71 yellow and 230 green seedlings. In subsequent years progenies from selfs of heterozygous individuals gave ratios as follows: 192 yellow to 579 green; 18 yellow to 60 green; 26 yellow to 89 green; 33 yellow to 85 green seedlings. The totals are 340 yellow to 1043 green seedlings. This ratio is very close to the ratio of 345.75:1037.25 expected for one heterozygous pair of factors (Dev. 5.75, P.E. 10.85).

ROSETTED LEAF

A modification of the leaf blade (Fig. 1) which is here designated as rosetted leaf was first noticed in the F_2 of a cross between a summer squash and a gourd. Plants showing this character have the lower lobes of the leaf blades developed inward in a slight spiral giving an effect more or less like a rosette. The character shows considerable variation in its expression and is not always easy to classify. An examination of the parental lines resulted in the discovery that the character occurred in some plants of the gourd parent. In the F_2 of the cross 17 plants were classified as having rosetted leaves and 68 as having nonrosetted.

A cross was made between one of the plants with rosetted leaves (Fig.

*Paper from the Department of Botany and the Herbarium of the University of Michigan. Facilities for growing the lines and crosses were furnished by the Botanical Garden.

1) and a summer squash variety which does not have rosetted leaves (Fig. 2). The plants of the F_1 all developed nonrosetted leaves. A selfed plant of the F_1 gave 55 plants with rosetted leaves and 220 with non-rosetted.

A cross was also made between a plant of the gourd having rosetted leaves and a plant of a white-disk summer squash with nonrosetted leaves. All the plants of the F_1 developed nonrosetted leaves. A selfed plant of the F_1 gave an F_2 having 26 plants with rosetted leaves and 70 with non-rosetted. The three segregating populations produced totals of 98 plants with rosetted leaves and 358 with nonrosetted, which is close to the ratio 114:342 expected for a single pair of heterozygous factors (Dev. 16, P.E. 6.24).

HARD RIND OF FRUIT

In *Cucurbita pepo* the fruits of the gourds and some of the varieties of squash have a hard rind due to thick-walled stone cells of the outer mesocarp. In varieties of squash with a soft rind the walls of the cells of the outer mesocarps of the fruits are thin. A study of the inheritance of these characters was made in crosses given in Table I. Gourds A and

TABLE I
INHERITANCE OF HARD RIND IN THE F_2
OF CROSSES OF CUCURBITA PEPO

Cross	Hard rind	Soft rind
Gourd A \times White Disk	126	52
Gourd A \times Yellow Disk	53	20
Sweet Potato \times Gourd A	50	16
White Disk \times Crown Gourd	76	28
Prolific Straight Neck \times White Disk	53	19
Sweet Potato \times Prolific Straight Neck	81	30
Total	439	165

Crown and Prolific Straight Neck squash have hard rinds, and the three varieties of squash, White Disk, Yellow Disk and Sweet Potato, have soft rinds.

In all the crosses the fruits of the plants of the F_1 had hard rinds. The accompanying table gives the results obtained in a study of the F_2 of each cross. The ratio of 439:165 is close to the ratio of 453:151 expected for a single pair of heterozygous factors (Dev. 14, P.E. 7.18).

COLOR PATTERN OF FRUIT

The gourd which is designated here as Gourd A has a bicolored pattern (Figs. 3-4), the fruit usually having green and orange-yellow transverse zones. The relative proportions of the zones vary considerably even on the fruits of a plant. Usually there are two zones, but occasionally more than two occur. Some fruits may be mostly green, with only an orange-yellow blotch (Fig. 3). In extreme variations the fruits may be all green (Fig. 4) or all orange yellow. In addition to the bicolored condition, there is a longitudinal striping in which the color of the stripe, either green or yellow, is of a lighter intensity than the ground color (Figs. 3-4).

Gourd A was crossed with a summer squash, variety Zucchini, which is entirely dark green (Fig. 5). The F_1 plants usually produced fruits which were bicolored and without longitudinal stripes (Fig. 5). Fruits of plants showed considerable variation of the bicolored condition. Fruits with definite zones, green except for an orange-yellow blotch, and all green, frequently occurred on a plant. The two latter conditions were more common in these plants than they had been with the parent, and in some plants they were the only conditions. No plant was noted which had all yellow fruits.

The F_2 obtained from selfed plants of the F_1 produced plants with fruits as follows: 162 bicolored without stripes, 53 bicolored with stripes, 28 yellow without stripes, 3 yellow with stripes, 103 green without stripes, and 33 green with stripes (Fig. 6). It is evident that longitudinal striping is inherited independent of the bicolored condition. The F_2 produced 89 plants having longitudinally striped fruits and 293 without striping. This is very close to the ratio of 95.5 : 286.5 expected for a single pair of heterozygous factors (Dev. 6.5, P.E. 5.71).

Sinnott and Durham¹ have reported in their studies that two pairs of factors are responsible for the inheritance of color of fruits in *Cucurbita pepo*. They find that the factor W is epistatic to Y, WY and Wy producing white fruits, wY yellow, and wy green fruits. Two types of striping are discussed. One is considered to be due to factors interacting with color factors to inhibit the expression of the epistatic factors in the areas of the stripes. Whether the stripes are yellow or green is dependent on the genotypes involved. They decide that plain white is dominant over

¹Sinnott, Edmund W., and Durham, George B., "Inheritance in the Summer Squash," *Journ. Heredity*, 13 (1922): 177-192.

white with green stripes with a single factor difference involved. They were not able to reach any conclusions concerning the relation of white with yellow stripe to plain yellow except that it apparently is dominant. In the other type of striping reported by Sinnott and Durham the stripes are of the same color as the body but deeper in shade. They consider that such stripes are probably produced through the effect of "the striping factor on those factors modifying the intensity of body color." This would imply that the factor involved is believed to be the same as that in the first type of striping. This would be expected to produce green stripes in the yellow portions of Gourd A. It would therefore appear that the factor for longitudinal stripes in Gourd A is different, operating directly on the body colors.

The inheritance of the bicolored condition when studied separately from striping gives a ratio in the F_2 of 215 plants having bicolored fruits to 31 having yellow, and 136 having green. The occurrence of plants with all yellow fruits in the F_2 of the Gourd A cross suggests that the bicolored condition may be due to more than one pair of factors. The extreme variability of the bicolored condition makes it very difficult, however, to reach a conclusion. Some of the plants included in the bicolored class produced all-yellow fruits together with bicolored fruits. Since the plants included in the yellow class each produced only one fruit, their identity and accuracy of classification are questionable. The same is true of single-fruited plants placed in the green class. It is possible that a single dominant factor is responsible for the bicolored condition and that the variability of its expression is responsible for the deviation from the ratio which would be expected.

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EXPLANATION OF PLATE I

Inheritance in *Cucurbita pepo*

FIG. 1. Leaf showing rosetted condition

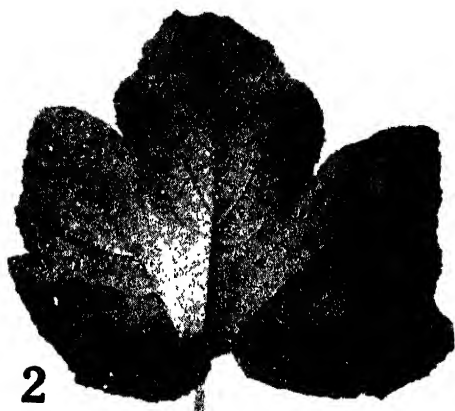
FIG. 2. Leaf of a type commonly found in *Cucurbita pepo*; nonrosetted

FIG. 3. Four fruits taken from a plant of Gourd A, showing variation in pattern

FIG. 4. Three fruits taken from a plant of Gourd A. Note that the one to the right is entirely green

FIG. 5. Fruit to the left from Gourd A parent, middle fruit from Zucchini parent, fruit to the right from a plant of the F_1 of the cross Gourd A \times Zucchini

FIG. 6. Some of the types found in the fruits of the F_2 of the cross Gourd A \times Zucchini, reading left to right: bicolored with longitudinal stripes, bicolored without stripes, green with longitudinal stripes. All-yellow fruits with and without stripes were also obtained



Inheritance in *Cucurbita pepo*

REPRODUCTION OF *ACROSYPHYTON* *CARIBAEUM**

WM. RANDOLPH TAYLOR

DURING the spring of 1949 the writer undertook at Bermuda certain morphological studies of marine algae and also made a general survey of the algae about the islands. Since some peculiarly interesting Rhodophyceae not readily available on the mainland were accessible there, these received his first attention.

Acrosymphyton has been separated from *Dudresnaya* on the basis of special features of the carpogonial apparatus of *A. purpurifera*. It was known (Sjöstedt, 1926) that *D. caribaea* should accompany *D. purpurifera* into the genus *Acrosymphyton*, because of the position of the auxiliary cell, but the development of its reproductive structures has not previously been made the subject of careful research and, since this plant was found at Bermuda (although rare), advantage was taken of the opportunity to make a thorough study of it, so that it could be compared with *A. purpurifera*, the only species so far completely studied. Through the courtesy of the curator at the New York Botanical Garden, Dr. D. P. Rogers, the writer was able to review the Collins and Howe specimens; and Dr. W. L. White, of the Farlow Herbarium, kindly loaned plants collected by Hall and Farlow. This has permitted considerable correction of herbarium determinations of plants of these two genera, respecting the American records.

One of the notable species of Rhodophyceae reported as among the features of the Bermudian flora is *Acrosymphyton caribacum*. The plants are bushy, with prominent leading and secondary axes reaching a height of 16 cm. or more, though commonly less. The branching is

* Contribution from the Department of Botany, University of Michigan, No. 917, and from the Bermuda Biological Station for Research, No. 163.

This work was facilitated by a grant from funds placed at the disposal of the Bermuda Biological Station by the American Philosophical Society. For this generous aid, and for the very cordial coöperation of the former director of the Station, Dr. D. E. S. Brown, and of his assistant under the grant, Mr. Albert J. Bernatowicz, the writer is exceedingly grateful.

rather regularly radial, of 5–6 successive degrees. Reported distichous branching is probably an artifact produced by flattening these highly gelatinous specimens for drying or the result of a slight occasional tendency to fasciation. The main axes may reach a diameter of 5–8 mm., but are usually much less; the ultimate ramuli are generally exceedingly slender, one millimeter or less in diameter, long and sharply tapering. In color they are dull when living, but when dried are a stronger rose red. This plant has been found at but a very few stations, where it seems to have the same growth habits as *Dudresnaya crassa*.

Acrosymphyton caribaeum was represented in the herbarium of the New York Botanical Garden by five specimens under the name *Dudresnaya caribaea*. One, from Bermuda, was sterile; three from Dry Tortugas, Florida, and one fragment from Miami Beach, Florida (of which the major portion was in the writer's herbarium), were confirmed as *A. caribaeum*. To these must be added ten erroneously placed in *D. bermudensis* (including two issues of Phyc. Bor.-Amer. no. 2195), all Bermudian except one from Great Bahama Island. Since the two Garden copies of the Phycotheca specimens, one of which was Collins' own, and those in the sets belonging to the University of Michigan and the writer are incorrectly identified, the implication is that all specimens of Phyc. Bor.-Amer. no 2195 are to be mistrusted.

It is necessary to remark here, parenthetically, that the observation made above regarding the misidentification of specimens labeled "*D. bermudensis*" does not imply any invalidity in the species itself. A small specimen in the Collins herbarium labeled "Dud #2" (in pencil) and "*Dudresnaya bermudensis* from the type material" closely resembles the photograph of Setchell's type plant, and when examined microscopically conforms to his definition in the essential points of peripheral filaments and auxiliary branch. Presumably it comes from the Farlow material of 1881. While the vegetative filaments of *D. bermudensis* resemble those of *A. caribaeum*, the reproductive structures clearly show that the relationship is with *D. crassa*. Setchell's description (1912, p. 244) does not seem to the writer to be correct, for he states that "From *D. crassa* it differs . . . [by] the absence of a single specialized (smaller) auxiliary cell in each auxiliary branchlet." Material properly expanded with a solution of caustic potash showed that the auxiliary cell was decidedly smaller than the neighboring cells, which reached 15 μ diam., though possibly the whole branch was shorter and much blunter, and the cell distinctions somewhat less than those in *D. crassa*. The obovoid cells

of the peripheral filaments decreased for the outer 3–4 divisions; in the cells near the surface the diameter was 5.4–7.5 μ .

Acrosymphyton caribaeum was not as abundant in 1949 as was *Dudresnaya crassa*, but excellent fertile material was eventually found on one occasion, as well as a very few sterile plants. In branching, in gelatinous character, and in general structure there was little to distinguish these plants from those of *Dudresnaya*. Perhaps in young plants there was more difference in diameter between the ultimate and the main branches, and the young branches probably tapered to more delicate tips, but in old specimens this was not evident. In both the basic structure consists of a series of very large axial cells, each bearing somewhat above the middle at first two, later four, repeatedly branched vegetative ramuli, completely enveloping the axis. The axial cells in our material reach a diameter of at least 60–130 μ ; they are supplemented by slender (7.5 μ) rhizoidal outgrowths from the lower cells of the vegetative ramuli. These ramuli branch repeatedly, depending on the age of the part examined, and the cells are progressively supplied with more chromatophores as one approaches the surface. At the time that reproductive structures are forming they have subdichotomously forked 5–7 times at moderate angles, the cells rather more elongated in the lower series and often subfurcate on the end, but the cells toward the surface are broadly obovate and about 6.5–10.0 μ diam. (Fig. 4).

The irregularly rounded spermatangial clusters develop abundantly on the outer divisions of the vegetative branchlet systems in male plants, replacing the ultimate divisions. Branching here is no longer dichotomous, but irregular to subopposite (Figs. 1–3).

Carpogenic branches were not difficult to find, though less abundant than in *Dudresnaya crassa*. The difficulties lie in interpreting them when they are found, for their growth habit is very likely to obscure the important characters. They first appear as a short row of cells near the base or a vegetative branchlet, as a division of a dichotomy or a trichotomy. They are distinguishable by failure to fork immediately like the vegetative ramuli; the cells remain short. The little initials, when about 5–7 cells long, begin to curve, and may show signs of developing side branchlets of their own (Figs. 5, 10). With growth the curvature becomes greater, and the side divisions curve inward. Except near the carpogonium and near the base each cell may have an opposite pair of these, which become 3–4 cells long (Figs. 6–8). The carpogonium is at first simply oval; later the trichogyne becomes more narrow and elon-

gates, while the curvature further increases (Figs. 6-11). The whole structure is so crowded and confused by these curvatures that it is only the exceptionally well-flattened carpogenic branch which can be used for an illustration. The figures given are by no means average in this respect; they are particularly clear selected examples. The trichogyne, at first pointed down the branch, eventually curves outward toward the surface of the plant.

Fertilization is promptly evidenced by the more wrinkled aspect of the trichogyne and the appearance of a connecting outgrowth or primary oöblast from the carpogonium. This is turned or soon swings down the inner face of the carpogenic branch (Figs. 12-13). In its progress it fuses with one or more of the terminal cells of the side ramuli. The terminal cells are little differentiated, being merely rounded and somewhat larger than the others. These cells are doubtless nutritive in function, rather than auxiliary ones destined to produce cystocarps; in rare instances (Fig. 15) one of them by its isolation and size suggests that it is actually a potential auxiliary. No examples of effective functioning of such aberrant auxiliaries were observed. After the initial fusion of the outgrowth from the carpogonium, extension and further fusions occur (Figs. 14-16). At least three or four of these end cells, as well as others, may become involved. It was occasionally noted that, in addition to the lateral ramuli from the carpogenic branch, one-celled outgrowths could develop from the inner face of these laterals, and from the axis itself, and could become involved (Fig. 11). As the process advances, the cell contents become less dense, and eventually the whole seems impossible of interpretation, even by the use of stains. Fortified by the fusions on the carpogenic branch, one or more true oöblasts are produced which strike out in various directions from the fusion mass, potentially to connect with auxiliary cells at some distance in the plant, and to initiate carpospore formation (Fig. 15).

The auxiliary cells in *Acrosymphyton caribacum* are terminal on their axes, and when mature are quite distinct, but large and with more sharply defined walls rather than especially dense with stored food. Axes arise on the lateral vegetative ramuli, generally equivalent to one side of a fork. The other, vegetative, side far outstrips them before their identity can be distinguished (Fig. 18). Then their short, stout, rather dense cells mark them out. With subsequent growth of the vegetative ramuli additional auxiliary axes may be produced (Figs. 19-20) until there may be several. The length varies much, the functional axes having from

5 to 12 cells (Figs. 20, 28), but doubtless more extreme examples could be found. The diameter is about 8–12 μ ; that of the terminal auxiliary cell, about 12–14 μ . The auxiliary axes are typically unbranched, but occasionally lateral branchlets are seen which have no special function (Figs. 21, 23). Division of the axes into several functional branches is not rare. As many as seven potential auxiliaries were seen on one axis (Fig. 22), and numerous cases were noted in which more than one of these could function (Fig. 17). Generally the picture was then so confused that no reproducible drawings could be made.

The true oöblast, on making contact with an auxiliary, seems generally to attach and fuse with the side of it. The auxiliary promptly elongates axially, the bulk of the cytoplasm passes to the distal end, and the oöblast grows out again from the point of contact to continue toward other axes (Fig. 26). It was quite possible to follow these succeeding contacts and fusions. We may have them between auxiliaries on the same forked axis (Fig. 17), where one has already formed carpospores while the other has only begun, or, more commonly, with relatively distant auxiliary axes (Figs. 24, 25) where the bridging oöblasts usually remain to show the connection. Though not figured, the oöblast from the fusion cell in Figure 16 was traced through four attachments to independent auxiliary branches, the first and fourth producing normal cystocarps but the other two seemingly sterile. It proceeded yet further in the plant. Cross walls in the oöblasts were generally formed some distance behind a point of fusion, and eventually in the extension at a similar distance, but were by no means consistently discernible.

The cystocarp is initiated from the protoplasm-rich elongated upper part of the auxiliary fusion, where a cell is separated by a cross wall close above the level of the oöblast attachment. This cystocarp initial cell is thus distinctly denser than the rest of the structure, which contains little protoplasm. The subsequent irregular divisions (Fig. 27) produce a relatively small mass of large dense carpospore cells (Figs. 17, 28). The further history in this plant is uncertain. As in *Dudresnaya crassa*, tetrasporangial plants are unknown, and there is no morphological clue to the occurrence of meiosis in any definite alternative place. Critical cytological work is needed in both instances to show the true nuclear conditions, and this will be difficult, though not impossible, because of the gelatinous nature of the species.

Our first substantial account of the reproductive apparatus of *Acrosymphyton* appears in the work of Bornet and Thuret (1867, p. 156) on

A. purpurifera (as Dudresnaya). They correctly portray carpogenic and auxiliary branches. They also recognize, if a bit imperfectly, a primary fusion within the carpogenic branch and communication by slender filaments between this and successive auxiliary cells, with subsequent cysto-carp formation. The delineation of structures is, as one would expect from Édouard Bornet, exquisite. Schmitz (1883, p. 255) and Berthold (1884, p. 12; pl. 5, fig. 1) add nothing to these microscopic observations, but the latter figures the plant excellently. Oltmanns (1898, p. 101) reported on stained material, and so his figures show some distortion; his comprehensive text (1922, p. 387) adds nothing of moment. More clearly than his predecessors he recognized the morphology of the primary fusions on the carpogenic branch and formulated ideas still current regarding the transfer of nuclei to the auxiliary cells, but he did not take up the problem, so important here, of chromosome reduction in the general absence of tetrasporic plants. Sjöstedt (1926, p. 8) recognized the importance of the differences between these reproductive structures and true Dudresnaya by segregating in Acrosymphyton the species *purpurifera* and *caribaea*. The present study shows the general similarity between these two species, though some differences appear. Kylin (1930, p. 22; 1937, p. 211) gives a new set of figures, but his description follows the established line. The great disproportion which appears between carpogenic branch and auxiliary filament in *A. caribaea* does not appear in *A. purpurifera*, and the auxiliary branches which he figures as of 5-6 cells are certainly much shorter than those of *A. caribaea*. Feldmann (1942, p. 236) confirms some points respecting *A. purpurifera*, but adds no new data. Oltmanns noted development of three connecting outgrowths from the carpogonium, one fusing with the end cells of each lateral set of branchlets and the third with superficial cells near the axis, though this one might be absent. We generally find only one connecting outgrowth in *A. caribaea* (Fig. 4), though sometimes there are two (Fig. 7), but no more, and in no case are they cut off by a cross wall at their point of origin, as Oltmanns and Kylin clearly figure for *A. purpurifera*. The one or, occasionally, two outgrowths characteristic of *A. caribaea* initiate a large general fusion cell on the concave side of the carpogenic branch, without cross walls, instead of the compartmented structures which he figures. In both species of Acrosymphyton there are few, usually one or two, oöblasts formed from each carpogenic branch, and few secondary oöblasts from the points of junction with auxiliaries. Espe-

cially in the first feature this is very different from the condition in *Dudresnaya crassa*.

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EXPLANATION OF PLATE I

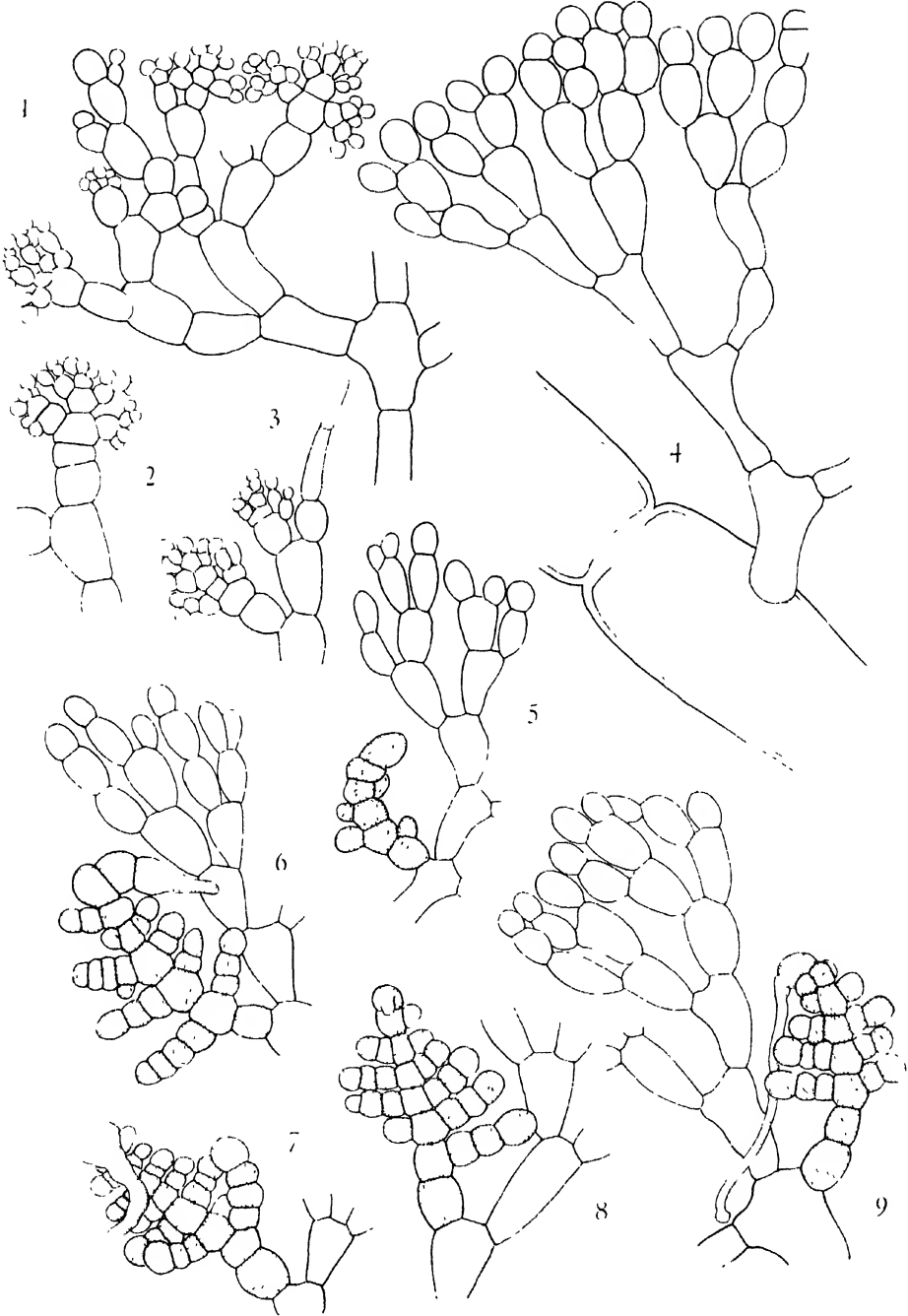
Acrosymphyton caribaeum

(All figures $\times 575$)

FIGS. 1-3. Tips of assimilatory branches bearing clusters of spermatangia

FIG. 4. Well-developed assimilatory filament cluster on an axial cell, previous to the formation of secondary longitudinal filaments

FIGS. 5-9. Stages in the development of carpogenic branches, shown attached to the lower cells of young assimilatory filaments. In Figure 5 lateral ramuli have just begun to appear and the carpogonium is undifferentiated, but the axis is already curved. Figures 6, 7, 8, 9 show successive increases in the development of the lateral ramuli and elongation of the trichogyne

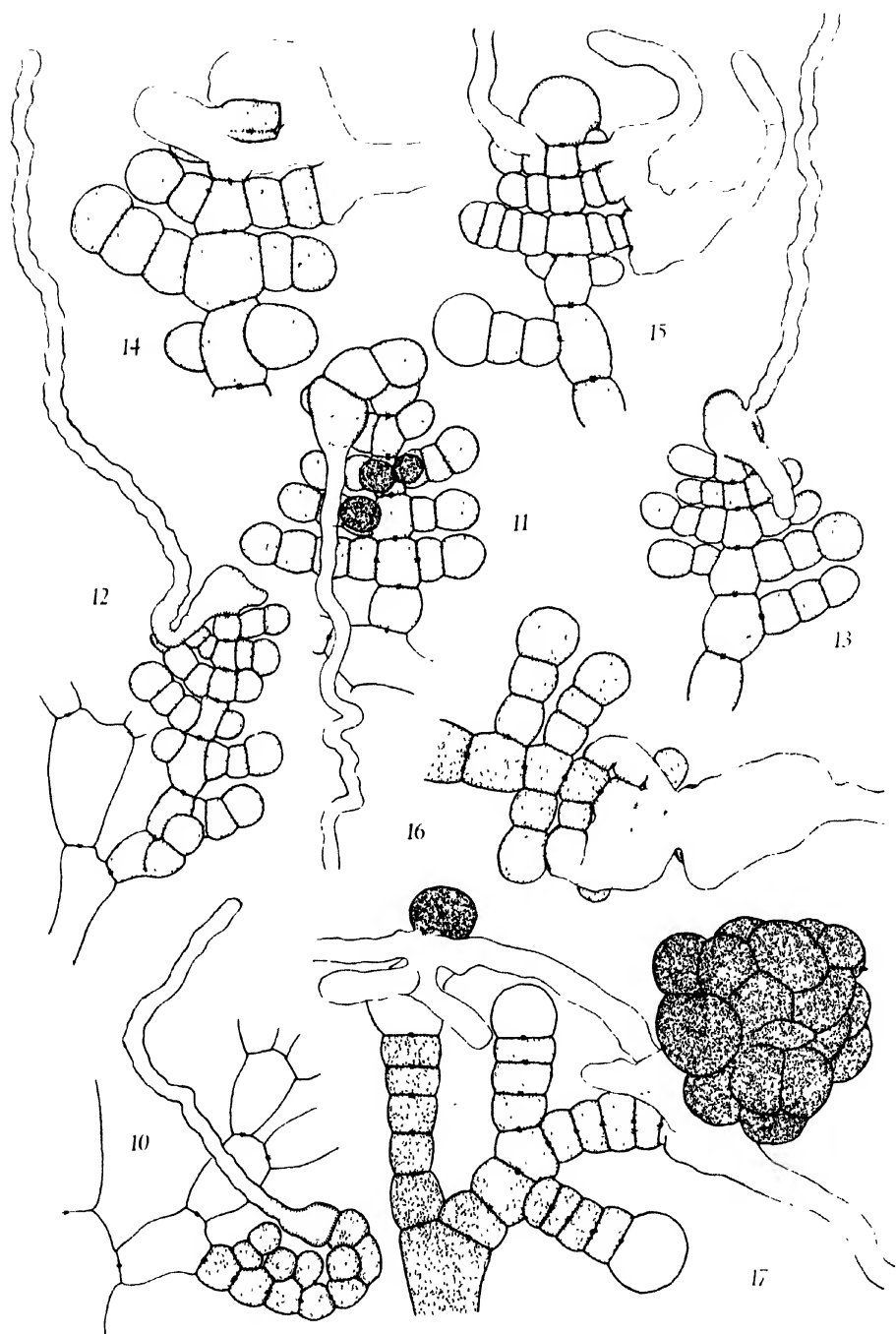


Reproduction of Acrosymphyton

EXPLANATION OF PLATE II

Acrosymphyton caribaeum

- FIG. 10. Relatively young carpogenic branch, the trichogyne well developed but the lateral ramuli rudimentary. $\times 575$
- FIG. 11. Mature carpogenic branch. On the face of the branch are shown certain special cells (three darker-shaded, two more under the carpogonium and shown in outline only) formed at right angles to the plane of the lateral ramuli. $\times 1000$
- FIG. 12. Carpogenic branch after fertilization. The initial of the connecting outgrowth appears as a prolongation of the right-hand angle of the carpogonium $\times 755$
- FIG. 13. Carpogenic branch after fertilization. The outgrowth runs down the face of the branch. $\times 755$
- FIGS. 14-16. Examples of the fusion of the connecting outgrowth with nutritive cells of their respective carpogenic branches. While it is usually the enlarged terminal cells of the ramuli which become involved, one notes in Figure 14 fusion with an axial cell, and it is quite probable that more than terminal cells are involved in Figure 16. In Figure 15 a lower cell of the carpogenic branch bears what appears to be a true auxiliary cell. Figure 14, $\times 752$, Figures 15-16, $\times 1000$
- FIG. 17. A branched auxiliary ramulus, showing two of the four auxiliary cells activated. The oöblast after fusing with that on the right has initiated another cystocarp, which is still in the one-celled stage, on the left $\times 725$

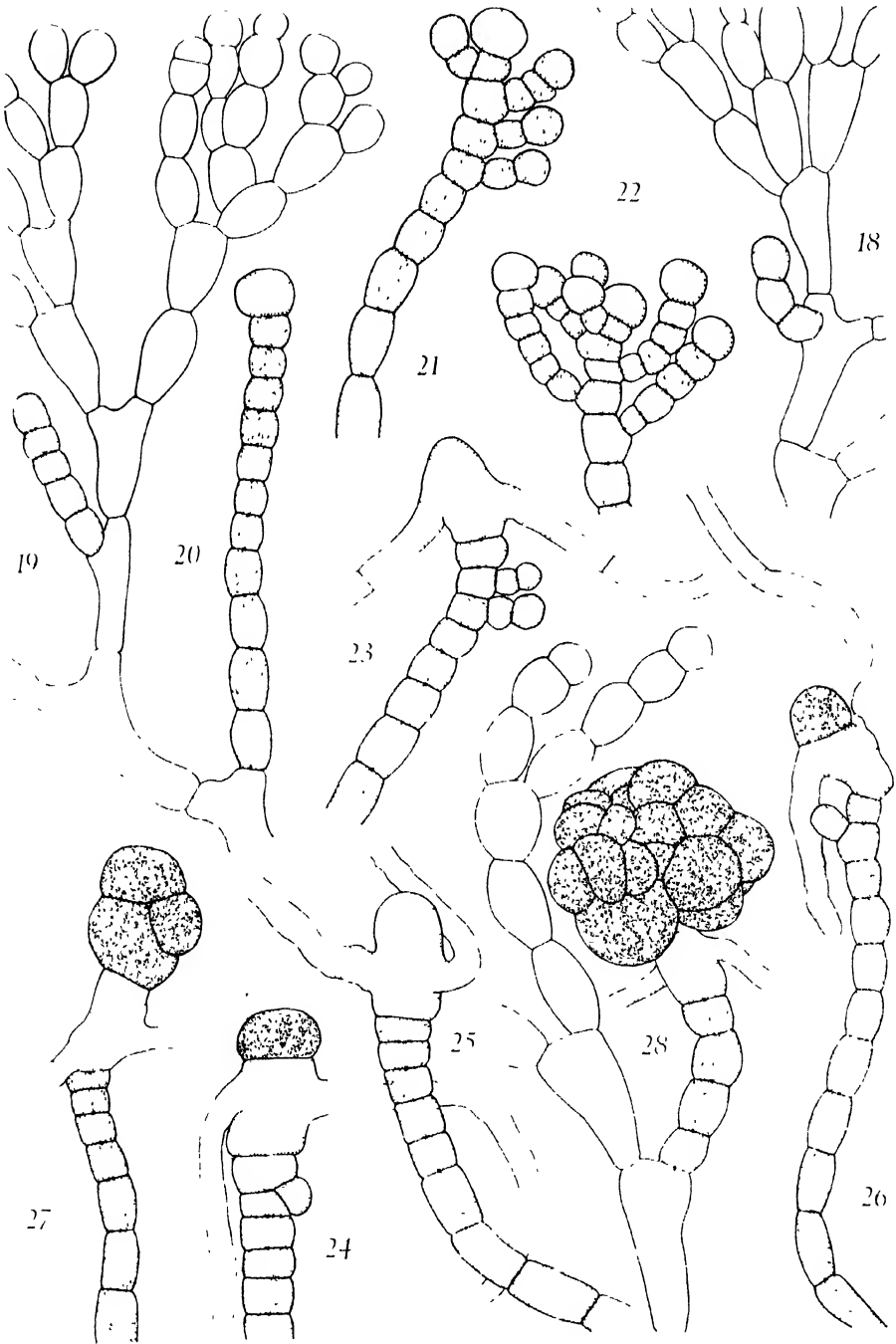
Reproduction of *Acrosymphyton*

EXPLANATION OF PLATE III

Acrosymphyton caribaeum

(All figures $\times 575$)

- FIGS. 18–20. Stages in the development of auxiliary branches on assimilatory filaments. As Figures 18–20 show, there is commonly a succession in one assimilatory cluster. The terminal unshaded cell is the mature auxiliary
- FIGS. 21–22. Auxiliary branches which bear lateral ramuli. In Figure 21 they appear to be sterile, but in Figure 22 all seven apices appear to bear potentially fertile auxiliaries
- FIGS. 23–25. Auxiliary cells to which oöblast filaments have recently fused
- FIG. 24. Formation of the first initial cell of the cystocarp. This branch was directly connected by the same oöblast with that shown in Figure 25
- FIG. 26. Formation of the initial cell of a cystocarp
- FIGS. 27–28. Stages in the formation of the cystocarp



Reproduction of *Acrosymphyton*

VASCULAR DEVELOPMENT AND TRANSITION IN *ECHINACEA PURPUREA*

JAMES WILLIAM UNGER

INTRODUCTION

ECHINACEA PURPUREA (L.) Moench is a member of the Compositae, series Tubuliflorae, tribe Heliantheae. A considerable amount of morphological work has been done upon members of the Compositae in relation to the flower ontogeny, the type of megagametophyte, the embryo development, and the vascular transition in the seedling. There are, however, few accounts of embryogeny and seedling differentiation within a given species. Miller and Wetmore (1945) traced the ontogenetic development of *Phlox drummondii* from the megagametophyte through the differentiation of the seedling and the maturation of vascular elements. The present paper is part of a morphological study of the development of a species of Echinacea from the origin of the floral parts through seedling development and vascular transition.

Esau (1943) summarized the early vascularization of embryos and seedlings with the conclusion that, while much work has been done on the development of the embryo, few investigators have been concerned with the manner in which the early vascular system of the embryo is blocked out. Nast (1941), in her paper on *Juglans regia*, explained that vacuolation of the cells in the pith and cortex of the hypocotyl and root delimits the future vascular regions of embryos even before the cotyledons are present as separate structures. Phillips (1937), working on *Cynara* seedlings, concluded that early vascular tissue appears near the base of the cotyledons and differentiates acropetally and basipetally from that level into the hypocotyl and the upper cotyledons. Miller and Wetmore (1945), in a study of *Phlox* embryos, found that the xylem appears first in the cotyledons and matures down into the hypocotyl and up into the cotyledons; the phloem differentiates in a similar manner but appears later than the xylem.

Papers are available dealing with vascular transition in seedlings of the Compositae, beginning with the work of Van Tieghem in 1870. Lee

(1912) studied seedling anatomy in about fifty species of the Compositae. Havis (1935) traced the transition from root to typical stem structure in *Tragopogon porrifolius*. Siler (1931) worked out the account of vascular transition in the seedling of *Helianthus annuus* and *Arctium minus*. Similarities may be noted in the development of these species, but it is difficult to state definitely a specific method of transition which is constant for the Compositae as a family.

MATERIAL AND METHODS

The floral buds of the purple cone flower and stages from flower to mature seed were collected from the arboretum of the University of Wisconsin during the months of July, August, and September, 1947. The material was fixed in formal-acetic-alcohol and in Craf's modification of Nawaschin's solution. Mature seeds were stored under refrigeration as a means of preservation and were germinated upon wet filter paper in petri dishes. Seedlings of different ages were selected for fixation, were dehydrated by a butyl alcohol series, and imbedded in paraffin (58°–59° C.). Serial longitudinal and transverse sections were cut at 10–15 microns. Most of the seedlings were stained with safranin and fast green. Root-tip smears were made by the use of aceto-orcein to determine the chromosome number of the plant.

THE DEVELOPMENT OF THE SEED AND SEEDLING

The mature embryo in the seed is uncurved and ranges from 3 to 3.5 mm. in length. The hypocotyl is short, and the cells composing it are unelongated until suitable moisture brings about growth and the fruit coat is cracked. The cotyledons are much longer than the hypocotyl and make up the greater portion of the embryo in the mature seed. No trace of suspensor remains at maturity.

It is possible to assign an approximate stage of development to the young embryo in the immature seed by observing the amount of integumentary tissue persisting. The integument gradually becomes collapsed as the embryo enlarges and the endothelial layer is obliterated. A mature embryo is surrounded by only the outer few cell layers of the integument.

At the time that the embryo has reached a stage of development equal to about two thirds its maximum size in the seed, considerable elongation of two layers of cells beneath the epidermis of the cotyledons indicates an early palisade development. The layers are located on the

abaxial side of the cotyledon and eventually become the photosynthetic tissue on the upper surface of the cotyledon after it emerges from the soil. At this age the hypodermal layer of cells shows an increased number of longitudinal divisions and great elongation in the longitudinal plane that results in a layer of narrow palisade cells. The second layer is not so conspicuously elongated as the upper. The remainder of the cotyledonary mesophyll is a tightly packed region of parenchyma that is somewhat thicker than the spongy tissue of a foliage leaf. The spongy parenchymatous nature of the mature foliage leaf is lacking in the cotyledons, and no stomata are formed in the epidermis at this age.

The earliest indication of vascular differentiation in the immature embryo is noted when it has reached the length of about 700 microns. The cotyledons average 395 microns in length at this stage. A light staining area, which is the first indication of a pith, is prominent just below the unelongated epicotyl. Outside this region and extending up into each cotyledon is a more heavily stained area that delimits the location of the provascular strands. The cells of these strands are less highly vacuolate than the pith cells and those that will contribute to the cortex. The inner layer of the cortical region is composed of cells similar in size to those of the provascular tissue. By tracing the histogens of the root tip from the lower end of the hypocotyl upward into the cotyledon it is possible to follow the line of separation between the cortex and the stele.

An embryo measuring 2.6 mm. in length shows slightly more development of provascular tissue in the cotyledons and the upper hypocotyl, as is indicated by the elongation of cells in a narrow region just within the inner layer of cortex. The cell elongation is slight, but the prominent nuclei and vacuolation in the cells of the provascular tissue further aid in making it distinguishable. In cross sections of the hypocotyl certain strands of the procambium are more sharply delimited than others, and the number varies according to the level in the embryo. The strongly developed strands of the procambium will become the future phloem strands. The xylem strands of the hypocotyl and the cotyledons are much less sharply delimited at this time, and the portion of the procambium from which they will be formed resembles areas of parenchyma that are alternate with the developing phloem through most of the hypocotyl. These become collateral with the phloem of the upper cotyledons in later stages. A pith is present in the upper hypocotyl, and the procambium is in the form of a dissected cylinder. The upper hypocotyl has a provascular cylinder of greater diameter than the lower levels, and three strands

are evident that are continuous with the developing strands in each cotyledon. The endodermal cells are enlarged at this age and are most distinct outside the areas of undeveloped phloem.

Embryos dissected from mature seeds give conclusive evidence of the plan of vascular development. At this time the phloem and xylem show the first sign of maturation. All evidence indicates that the maturation of the first phloem elements in a mature seed first begins near the base of the cotyledons and proceeds acropetally and basipetally from that region. The cell walls in the portion of the procambium from which phloem matures are most distinct at this level, and the nuclei of the cells in these developing phloem areas are large and granular in contrast to those of cells in the hypocotyl, root, and upper cotyledons. The walls of the immature phloem cells fit closely together. Frequently intercellular spaces are present in the cortex outside the phloem, and these spaces are continuous with spaces in the lower root area.

The origin of the protoxylem is more difficult to determine. Immature xylem cells become evident in the mature seed at a level in the lower part of the cotyledons. They may be identified by a decrease in the amount of protoplasm in a few cells of the provascular strand. These early xylem cells are similar in shape to the parenchyma surrounding them, but are distinguishable from the parenchyma by a shrinkage of the cell contents and a thickening of the primary walls. This characteristic has been seen in more than one series and represents the first visible step toward maturation.

In seedlings twenty-four hours after germination has begun the provascular strands in the upper hypocotyl increase in diameter by longitudinal divisions of cells, particularly in the inner portion of the strands. As viewed in transverse section, these divisions are periclinal and result in radial rows of cells. One of the cells in the innermost radial row, at the level of the lower cotyledon, begins to develop a secondary wall thickening, and the primary wall stains deeply. Cells of this type constitute the first mature xylem elements and develop annular and spiral lignified secondary wall thickenings. The nucleus disintegrates during the time that secondary wall formation is going on; in some seedlings this is followed, twenty-four hours after germination, by the complete disappearance of the protoplast. The end walls of these elements are slightly oblique and in close contact with other similar cells in a continuous row. Several fully matured rows of protoxylem and early metaxylem elements were observed near the base of the cotyledons within twenty-four hours

after germination had begun. From this time on the xylem development takes the lead over the phloem, and in forty-eight hours spiral, annular, and scalariform metaxylem elements have matured into the lower hypocotyl and the upper limits of the cotyledons. Elongation of cells occurs just below the cotyledonary node of the seedling, and the procambial cells in this region are longer than those of the cotyledonary strands.

Adjacent to the first xylem elements of the upper hypocotyl the provascular strand continues to divide longitudinally and cuts off linear rows of narrow cells that in turn divide periclinally. Some of these cells, in the outer part of the strand, become enlarged and function as the phloem mother cells. Continued procambial divisions produce additional rows of cells between the xylem and the phloem mother cells that later mature into metaxylem, metaphloem, and cambium. The end walls of the early phloem cells are flattened, and occasional transverse divisions form cells that may again divide periclinally. Observation of one-, two-, and four-day-old seedlings fails to reveal the presence of mature sieve tubes, but this may be accounted for, in part, by the fact that sieve tubes are often comparatively indistinct in the protophloem. The other possibility is that phloem has not matured at this age. Companion cells accompany the sieve tubes in older seedlings, but in seedlings of 24–48 hours it is difficult to be certain whether the accompanying cell is a companion cell or the result of a recent procambial division. Mature sieve tubes were first positively identified by the presence of sieve plates in the cotyledons of eight-day seedlings. The earliest maturation may have occurred in seedlings between four and eight days old. A provascular strand develops acropetally into the first true leaf of eight-day seedlings, and the strand connects with one of the lateral bundles of the upper hypocotyl. At this age it is not possible to distinguish between the portions of this strand that will form xylem and phloem in the leaf.

As determined by chromosome counts made from cells of seedling root tips, the diploid number of chromosomes in *Echinacea purpurea* is twenty-two.

VASCULAR TRANSITION

In seedlings eight days after germination the xylem and phloem strands are sufficiently well matured to enable one to determine their orientation throughout the hypocotyl and the cotyledons. Large parenchymatous cells at a low level in the central part of meristematic root tip show the location of the future metaxylem before the first poles of pro-

toxylem appear. At a slightly higher level in the primary root two patches of cells which will mature into phloem develop. About two millimeters back from the tip the two root poles have each been established by the lignification of one vessel for each pole. Higher in the root the number of vessels increases to two or three, at this age, and the phloem areas are larger. The xylem vessels are five- to six-sided, and spiral or annular thickenings are found on the walls. Many of the larger metaxylem vessels have scalariform thickenings on the side walls. The primary root is diarch and exarch, and the two xylem arms are each made up of four or five vessels that alternate with two lateral bands of phloem (Fig. 1). The phloem is separated from the xylem by several rows of parenchyma, and a number of large cells in the center will later mature into metaxylem. The vascular tissue is bounded on the outside by a single layer of pericycle. At this age two prominent layers of cells bound the inner cortex over the areas of phloem. These cells arose in the embryo during a late stage of seed development by periclinal divisions of the innermost periblem layer. Over the xylem the inner cortical layer has not divided periclinally into two cells but remains one cell thick. Casperian bands, which characterize the endodermis, are located only on the walls on the inner layer of cells. Between the endodermis and next layer of cortex are found conspicuous intercellular spaces that extend far up into the hypocotyl from the meristematic root tip.

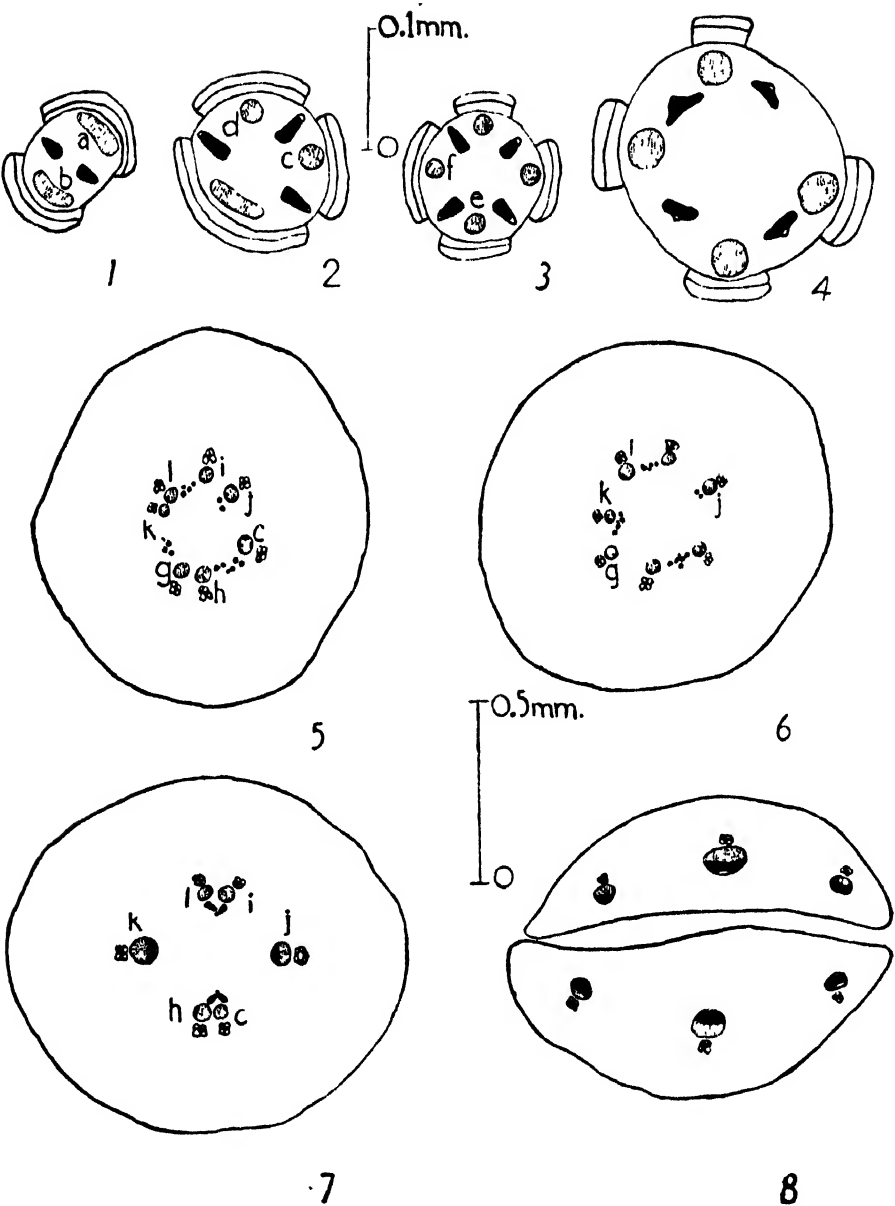
At a slightly higher level in the hypocotyl one of the two phloem areas (Fig. 1*a*) bifurcates into two new groups of phloem (Fig. 2*c, d*), and these groups start to separate from each other. A third exarch xylem arm differentiates radially between the two new groups of phloem (Fig. 2*c, d*). This arm is at right angles to the two original xylem arms of the root. The double arcs of inner cortical cells accompany the phloem groups in origin, so that outside each new phloem group is a separate arc.

At a level in the middle of the hypocotyl the second original group of phloem (Fig. 1*b*) bifurcates, and two new groups (Fig. 3*e, f*) result from the bifurcation. Farther up in the hypocotyl these groups of phloem separate, and a fourth xylem arm originates between them to establish a tetrarch condition (Fig. 3). The cortical arc remains one cell thick over the xylem arms and two cells thick over each group of phloem. Tetrarchy persists as far as the upper portion of the hypocotyl. The hypocotyl, therefore, is largely rootlike in structure. Up to this level the xylem is exarch and radially alternate with the phloem. Many pericycle cells at this level have very large nuclei and indicate clearly the possible origin of

secondary roots from the pericycle. The young branch-root primordia arise from the pericycle at different levels in a somewhat cyclic arrangement. An interesting point was noted in connection with this observation. Each primordium seems to be connected with the next one above in the hypocotyl by a series of pericyclic cells containing nuclei like those of the primordia. These nuclei are markedly larger than those of the usual pericycle cells.

The upper hypocotyl has a pith of greater diameter than the lower hypocotyl. The transition from root to stem structure is completed within the upper half of the hypocotyl. During this change of vascular orientation the metaxylem elements are differentiated laterally by a gradual "migration" at higher levels to each side of the protoxylem (Fig. 4). The vessels in each lateral group are closely associated at first and become separated from one another by parenchyma at a higher level. Two of the phloem groups (Fig. 2*d*; Fig. 3*e*) bifurcate at this level, each forming two new closely associated groups (Fig. 5*g, h* and *i, j*). This is followed, at a slightly higher level, by a bifurcation of the third phloem group (Fig. 3*f*) to form two separate groups of phloem (Fig. 5*k, l*). All of the six newly formed groups of phloem become further separated by parenchyma at successively higher levels, and three areas (Fig. 7*h, i, l*) together with one phloem group that does not branch (Fig. 7*c*) become associated with two groups of metaxylem to form two double bundles on either side of the stele (Fig. 7). These double bundles continue at higher levels as midribs of the cotyledons. In the cotyledon one of the remaining phloem strands (Fig. 5*j*) becomes collaterally arranged with xylem by the "migration" of both the xylem and the phloem (Figs. 6–7). This collateral bundle branches into two traces just below the level where the cotyledons separate from the hypocotyl, and each trace becomes a lateral bundle at the margin of each cotyledon (Fig. 8). A second lateral strand to the other margin of each cotyledon is formed at a higher level in the same manner as the first by the "migration" of xylem and a phloem area (Fig. 5*k*) located opposite the first lateral cotyledonary trace (Figs. 6–7). The one remaining unassociated phloem strand (Fig. 6*g*) continues upward in the hypocotyl and becomes continuous with the provascular strand that supplies the epicotyl and the first true leaf.

The conspicuous double arcs of inner cortex accompany each new phloem group in the upper hypocotyl, as was true of the root and the lower hypocotyl. The number of cells in each arc diminishes at higher levels until the usual number in the upper hypocotyl is four. The cytoplasm of



Figs. 1-8. *Echinacea purpurea*

the cells making up the arcs is dense, and these cells become the epithelium of resin ducts that develop schizogenously between the two cell layers. In the lower portion of the cotyledon the large double bundle is accompanied by two resin ducts laterally oriented in reference to the two patches of phloem. At a higher level the double bundles become collateral with the xylem, and the two ducts fuse so that only one duct accompanies the phloem (Fig. 8). Prior to the first branching of the midrib in each cotyledon another duct is formed in close association with the protoxylem. This second resin duct appears to arise from the bundle sheath. Each small lateral strand of the cotyledons has one duct associated with it until it reaches a point just below the place where it branches. At this location another duct appears opposite the first. The venation in the cotyledons corresponds to Lee's "Type 2" classification, in which three vascular strands "enter" the cotyledon, and the first branching in all three strands takes place near the base of the cotyledon.

EXPLANATION OF FIGURES 1-8

Figures 1-8 are camera lucida diagrams of vascular transition in *Echinacea purpurea*. Stippled areas represent phloem; solid areas, xylem

FIG. 1. Diarch root with alternating phloem (*a, b*) and exarch xylem. The double cortical arcs are external to two phloem groups

FIG. 2. Triarch region of lower hypocotyl after the bifurcation of one phloem area (*a*) into two new phloem groups (*c, d*) and the maturation of a third exarch xylem arm. Double cortical arcs are external to three phloem groups

FIG. 3. Tetrarch region of middle part of hypocotyl after a bifurcation of the second phloem area (*b*) into two new phloem groups (*e, f*) and the maturation of a fourth exarch xylem arm. Four cortical arcs are external to the phloem

FIG. 4. Lateral differentiation of the metaxylem in relation to the protoxylem at a level in the upper part of hypocotyl

FIG. 5. Bifurcation of three phloem areas (*d, e, f*) into six new phloem areas (*g, h, i, j, k, l*) and separation of these areas by parenchyma. The fourth phloem area (*c*) does not bifurcate. Resin ducts arise between the double layers of cortex external to the phloem

FIG. 6. Further "migration" of xylem and phloem to form two double bundles on the upper and lower sides and two collateral bundles on the left and right

FIG. 7. A level in the upper part of hypocotyl just before divergence of the cotyledons. The two double bundles continue as midrib bundles of the cotyledons and the two collateral bundles will split to supply each cotyledon with two laterals

FIG. 8. A level above the bases of the cotyledons, showing in each a large collateral midrib bundle derived from the double bundle. Two small laterals are in each cotyledon

The larger branches of the strands do not end blindly in the mesophyll but extend upward in a wavy course and reunite with the larger bundles at a higher level.

Starch grains are abundant in the cotyledons. A nongranular material is also present that stains easily with safranin. Further study should be spent on this species of plant to determine the nature of the inclusions present in the cotyledons.

DISCUSSION

The vascular differentiation in the embryo of *Echinacea purpurea* begins at a level in the base of the cotyledons. As stated earlier in this paper, Phillips (1937) noted that the first vascular tissue of *Cynara* seedlings matures near the base of the cotyledons and development then proceeds upward and downward. The phloem in the root is defined before the seedling stage is reached. The direction of vascular development of *E. purpurea* is similar to that in *Cynara*. In both of these species maturation of the xylem and phloem does not occur until after germination. In *Phlox Drummondii* (Miller and Wetmore, 1945), however, potential xylem can be recognized in the procambium of older embryos. The potential phloem arises from the part of the procambium opposite the xylem. By the time the mature seed stage is reached, adaxial procambial cells of the upper cotyledons have become mature protoxylem, and a few abaxial procambial cells in the lower cotyledons show characteristics of immature protophloem. The maturation of xylem and phloem is much earlier, therefore, in *Phlox* than in *E. purpurea*. A continuous row of mature protoxylem is established in the *Phlox* seedling that progresses up and down from the point of first maturation near the cotyledonary base. Protophloem cells mature in the same directions as the protoxylem.

The double bundle in the cotyledonary strands of seedlings is a common feature and becomes recognizable at different levels in different species of plants. According to Siler (1931), a double bundle is recognizable at the top of the hypocotyl in *Arctium minus* and extends into the midribs of the cotyledons. A double bundle is present in *Helianthus annuus* at the base of the hypocotyl and continues up into the base of the cotyledons. This study showed that *Echinacea purpurea* is not unlike *Helianthus annuus* in this respect. Several points of difference have been noted in the vascular differentiation of the root and the hypocotyl, however. The root of *Helianthus* is tetrarch in contrast to the diarch condition found in *Echinacea*. The triarch arrangement of the xylem in the

lower hypocotyl has not been described for *Helianthus*. Both are similar in developing six bundles of phloem by meristematic separation of pre-phloem at a higher level. Two of these areas become collateral with the xylem and provide lateral traces for the midrib of each cotyledon. In *Helianthus* two lateral traces are differentiated on either side of the double bundle, whereas only one trace is found on each side of the double bundle in *E. purpurea*. In *Arctium minus* the xylem is diarch in the root and in the hypocotyl. Six areas of phloem are delimited that supply the two lateral traces for each cotyledon and the double bundles in the cotyledonary tube. There are three collateral bundles in the cotyledon.

According to Havis (1935), *Tragopogon porrifolius* has a radial diarch root. The transition region is largely tetrarch owing to the formation of two bundles in addition to the two continuous with those of the root. These bundles are formed from metaxylem in the lower transition zone. The cotyledons have a collateral central bundle and two lateral strands; no double bundle is involved.

Thomas (1907) first used the term "double bundle" and reported that some Compositae have an "intermediate type" of venation in the cotyledons. She noted that the slender laterals on each side of the double bundle in the cotyledon fused with the corresponding laterals from the opposite cotyledon and began to form a tetrarch stele in the hypocotyl with the double bundles, but ultimately the laterals died out, so that the root was diarch. The vascular transition from cotyledon to root in *Echinacea purpurea* agrees in most respects with the type observed by Thomas. Hill (1913) added that such a type seemed to be confined to moderately large seedlings. Compton (1912) suggested that "triad" could be used more suitably than "double bundle" because such a bundle more closely resembles a triple bundle than a double one.

Lee (1912) outlined the vascular transition from root to stem in *Silphium*, *Xanthium*, *Heliopsis*, *Zinnia*, *Rudbeckia*, *Bidens*, and other members of the Heliantheae. He concluded that variations occur in even very closely related species, and sometimes in different individuals of the same species, a situation which indicates that "seedling anatomy is of no value in questions of affinity." All specimens that he studied were of the diarch or the tetrarch root type.

The two layers of cells external to the pericycle which are double over the phloem groups have been interpreted as endodermis by Siler for *Helianthus*. Phillips (1937) described the formation of a double-layered endodermis by a single periclinal division of the inner cortical layer. He

qualified the term "double endodermis," however, by pointing out that Casperian bands appeared only on the innermost cells of this double layer. Oil ducts arise from between the two layers of inner cortical tissue in the manner described for *Echinacea purpurea*. Inasmuch as Casperian bands appear only on the inner layer of cells in *E. purpurea*, the interpretation given in this paper is that the endodermis is one cell in thickness and that the two rows of cells making up the double layer have resulted from an early division of the innermost periblem cells. Williams (1947) has described the root tips of members in the Compositae and suggests that the endodermis functions as a cambium-like tissue that cuts off the linear rows of cortical cells found in many species of Compositae. He also called attention to the prominent intercellular spaces external to the phloem in many species. In *Echinacea* the cells of the middle and outer cortex are arranged in linear fashion with reference to the double inner layer. The manner in which the inner double layer over each phloem area stands out suggests that these cells become part of a continuous resin duct and that the lumen of this duct stems from the intercellular spaces between the two layers.

SUMMARY

Vascular differentiation begins when the embryo is about 700 microns in length. A dark-stained area extends up into each cotyledon and bounds a lighter staining area just beneath the epicotyl. This is the first indication of a pith.

An embryo of 2.6 mm. length shows a number of strongly developed areas in the procambium throughout the hypocotyl and the cotyledons. These strands later differentiate into phloem. The xylem strands are not delimited at this age. Endodermal cells are enlarged over the developing phloem areas.

The first immature xylem cells are evident in the lower part of the cotyledons in embryos dissected from mature seeds. Maturation of the first phloem element proceeds acropetally and basipetally from the lower levels of the cotyledon.

In twenty-four-hour seedlings the provascular strands of the upper hypocotyl increase in width by longitudinal divisions of the procambium. One or more rows of protoxylem and metaxylem mature into the lower hypocotyl and the upper cotyledons.

Mature phloem elements are first seen in eight-day seedlings.

The root is characterized by diarch, exarch xylem, and a radial ar-

rangement of xylem and phloem. At successively higher levels in the hypocotyl three and four xylem arms are differentiated. The hypocotyl is rootlike throughout the greater length.

At successively higher levels in the upper part of the hypocotyl the metaxylem becomes differentiated laterally in reference to the protoxylem, and bifurcation of three phloem groups provides the upper hypocotyl with seven areas of phloem. Four areas become associated with two laterally differentiated xylem arms and form two double bundles that become the midribs to the cotyledons. Two more phloem areas become collateral with the two remaining xylem arms and branch with the cotyledons to form a lateral bundle at the margins of each cotyledon.

Each strand of phloem in the root and the lower hypocotyl is bounded on the outside by a double arc of cells resulting from an early division of the innermost periblem. In the upper hypocotyl and cotyledons these double cortical arcs become reduced to about four cells, and resin ducts are formed by the schizogenous splitting apart of these cells.

As determined by chromosome counts made from cells of root tips, the diploid number of chromosomes in *Echinacea purpurea* is twenty-two.

ACKNOWLEDGMENT

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INCREASED MULTIPLICATION AND OTHER EFFECTS OF IRRADIATION ON TULIP BULBS*

TEUNIS VERGEER

TO DETERMINE the effects of slow neutron irradiation on plant materials a lot of 500 tulip bulbs of the early double variety Mr. van der Hoeff was gratuitously contributed by Dr. Willem E. de Mol, of Amsterdam, Netherlands. Of these 470 were irradiated. In nearly all instances the irradiation used permitted a certain amount of development. The plants survived for a variable length of time but eventually all died, leaving no viable offspring (1).

Thirty normal bulbs of the same variety had been packed and shipped in one container with 440 of the irradiated bulbs. The plants which developed from these 30 bulbs showed many marked modifications, which are reported in this paper. Whether these bulbs suffered secondary irradiation from the neutron irradiated bulbs or were irradiated in another manner cannot be positively stated at this time, but subsequent experimentation with gamma rays seems to support the first alternative (see below).

The 30 bulbs were planted outside on December 23. A commercially grown lot of the same variety which had been planted in the same field about 30 feet distant served as controls. Soil conditions, exposure, and fertility were identical so far as could be determined, but the commercially grown lot was planted about November 15. It is common experience among growers that planting at this late date makes very little difference in the time at which the tulips bloom and causes no marked modifications, but tends to reduce the crop.

Some of the experimental tulips developed more slowly than the controls. On the fourth of May, 26 of the 30 plants were above ground. One of these lacked a flower bud, two were only 2.5 cm. high, and 23 were

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10 to 15 cm. high. The flowers of six had developed to such an extent that the yellow color of the petals was pronounced and the diameters of the opening flowers ranged from 2.5 to 5 cm. The commercially grown lot of 150 bulbs, planted 38 days earlier, were about 20 cm. high at this time and had flowers about 10 cm. in diameter. The greatest flower development of the 30 probably was attained by May 12, although the plants were by no means uniform in this or any other respect.

LEAVES

On May 23, when normal plants of this variety were up to 24 cm. high, average 20.9 cm., the height of 24 of our plants ranged from 3 to 24 cm., average 16.38 cm. Except for the smallest plants, no leaf enlargement took place beyond this date. Three plants, nos. 16, 24, and 29, which had previously been used for study, were left or replanted, and three had not come up. One of them, no. 19, had 6.3 cm. of plant development above the bulb. Another, no. 17, had a mass of turgid leaves coiled up in the soil, and the third, no. 15, had two elongated internal buds protruding one fourth and three fourths of an inch above the bulb, which otherwise grew only 4.5 cm. and never reached above the soil. It had no roots and was replaced two inches deep in the soil. The roots of the other two were not investigated, but the 2.5 inches of soil above the underground growth was dug away, and the soil around the leaves was loosened in the hope that the leaves would reach light for photosynthesis. In spite of this, they did not grow above the soil.

Calorimetric methods were not available, but the general impression that the plants which grew to fairly normal size had rather normal chlorophyll development and that the leaves of plant no. 11 were a darker green than those of other tulips should be mentioned.

By May 31 the commercial lot of 150 tulips of the same variety had died down completely. On June 4 the 24 fairly well grown plants of the lot of 30 appeared healthier than ever. All other tulips in the same field, including thousands of Darwins, which normally mature two weeks after Mr. van der Hoeft, had died, with the exception of the variety Carara, which had leaves partly green and partly dried toward the tips. This is known to be a very late variety.

After the Carara and all the other bulbs had been harvested and the field plowed, our lot of Mr. van der Hoeft was still green and aroused much curiosity among growers. Most of them died in the last week of June. In fact, on July 2, when the bulbs were harvested, some of the

plant stems were still partly turgid. However, because of the necessity of making a report, harvesting was undertaken. A similar extension of the growth period was observed by De Mol in irradiated gladioli (2). As was to be expected, the longer photosynthetic period favored crop development (see below).

Modifications were common among the leaves. There were obvious differences in the spacing along the stem. Two plants, nos. 23 and 31, had leaves with the upper ends very blunt, curled, and torn. A dead brown streak was observed in the middle of one leaf of plant no. 20. Several had variegated leaves with reddish or whitish edges. The upper leaves at times were yellow-colored but turgid; at other times, half yellow, half red. One leaf was attached to the stem along one side. Four leaves were split 1.5 to 4 cm. from the apex toward the base. This occurs rarely in normal Mr. van der Hoeft and has been observed in the commercially grown bulbs in 3 per cent of the plants. Any of the variations mentioned may occur in normal plants, but the multitude of variations observed in this small group suggests abnormal influences.

STEMS

Mr. van der Hoeft is a very straight, stiff, and heavy-stemmed tulip, so that it is excellent for formal bedding. Five of the 21 fairly normal plants, however, had obviously crooked stems, most of which bent sharply at the soil-air level. This also appears to be an induced variation.

PISTILS

In 21 plants, pistils and a variable number of abnormally developed petals were observed. On May 21, nine days after most of the flowers had reached a state comparable to full bloom, a dozen or more pistils still appeared to be sufficiently turgid to attempt fertilization, although most of the petals had fallen. Though it is unfortunate that pollination was not carried out earlier, it is possible that seed resulted in three pods. Pistils may remain receptive to pollen as long as ten days after the petals drop, according to Dr. F. W. Went (personal conversation). It is remarkable, however, that enlarging ovules were observed on the outside of some pistils before pollination and on others within two days afterward.

This growth of ovules was not due to fertilization because a period of two days is insufficient for pollen tubes to grow down and insure fertilization. The lack of seed production in the majority of these also indicates that fertilization may not have occurred at all. A hormone response due

to pollination is not excluded as the possible cause of part of this ovule development. The data recorded in the tables show, however, that several pistils had undergone material enlargement before fertilization was attempted. Those which died soon after the petals were only 2 cm. tall, but those which were turgid on or about May 23 were at that time three or more centimeters tall. Formation of ovules on the outside of the ovaries must be attributed to irradiation disturbances.

On May 23 one of these "flowers," no. 23, had only dried parts. Of the remaining 20 flowering plants only four had normal pistils, nos. 3, 9, 13, and 27. They were still growing on June 4. By this time the pistil of no. 27 was 4 cm. tall; the others were somewhat shorter. All eventually dried, and in the capsules of nos. 3 and 27 a few half-sized but otherwise normal-appearing seeds were found. Between May 23 and 27 five pistils were observed to be healthy and growing but modified in various ways. No. 28 was so broadly fasciated at the top that the surface of the stigma measured 3.7 by 1.5 cm. Its length was 3.5 cm. Later it grew an additional 12 mm. in length and developed many healthy red ovules on the lateral surfaces and finally some small seeds.

On May 23 no. 2 had a split from which 16 enlarged healthy ovules protruded to the outside. The split continued to become deeper, and 12 days later more healthy ovules had become visible, but no seeds resulted. The pistil of no. 31 also developed many external ovules which noticeably enlarged, but the enlargement was unilateral. It caused the ovary to become much distorted, and eventually the part with the ovules broke loose. No seeds resulted. Marked splitting of the upper part of the pistil occurred in no. 30, but little further development took place.

On May 23 the pistil of no. 18 had the upper 7 mm. markedly swollen. The stigma was purplish blue, whereas light green is normal. The pistil of no. 25 appeared to be growing on one side but drying on the other. On no. 26 only the stigma was drying, and on no. 20 the stigma was dried out but the ovary was turgid. The pistil of plant no. 7 also appeared normal in shape, but its color was much lighter green than usual. The pistil of no. 10 was losing its color; the pistils of plants nos. 5, 6, and 11 were drying. Three other pistils, on plants nos. 12, 21, and 22, were dried out by this time.

It should be emphasized that none of the pistils of the 150 commercially grown plants showed any enlargement, in spite of the fact that all flowers were left to dry naturally. The staminoid petals of this variety are known to be sterile, so that self-fertilization is impossible. Many

other early tulips in the field were blooming at the same time as the commercially grown control lot. Therefore cross-fertilization was possible, but none of the 150 produced any seed. Since 10 of the 20 pistils of the experimental plants lived longer than usual and enlarged markedly while only three developed any seeds, and those abnormally small in size as well as in quantity, the author interprets the unusual development in the seven which produced no seeds as parthenocarpy, probably due to irradiation. Enlargement due to pollination effects should also be considered as a possible explanation.

Though fertilization is most likely the cause of seed production in the three experimental pods, the slight amount of seeds and the obviously unusually small size raise the question whether they could be haploid. All seeds have been sown. If they grow, we might get plants with 12 chromosomes instead of 24, which is the known number of Mr. van der Hoeft, according to Dr. W. E. de Mol (personal communication). The univalent condition may also reveal unknown recessive characteristics and may provide a clue to the original species from which Mr. van der Hoeft and related tulips have been derived. Since some seeds formed in three pods, we assume that all other ovaries which enlarged were completely sterilized by the secondary irradiation.

PETALS

In general, petal development was also decidedly abnormal. The normal petal color of this variety is almost uniform light yellow, subject to fading to white. Plant no. 7 had some petals with considerable reddish-brown pigment at the upper edges and others in which this pigment extended halfway down the petals. No. 9 still had turgid outer petals on May 24. They were greenish except for a brown central patch and whitish edges, often lined with a fine brown feathered stitching. The inner petals (staminoid) had all the distal halves dried, but the proximal halves were still turgid. In no. 12 a few outside petals also were still turgid on May 24. They were predominantly yellow on the inside with white edges, but green on the outside. The petals of no. 13 were similar, but had brownish edges instead of white. The inner petals seemed badly scorched; the outside ones were turgid.

ASEXUAL REPRODUCTION

The most remarkable phenomenon displayed by these tulips deals with vegetative reproduction. Unfortunately, no exact records on the

normal rate could be obtained from the commercial growers, though all agree that it is very low as compared with those of other tulip varieties. Schoonoord, a sport of Murillo, from which Mr. van der Hoeft is derived, is also an early double variety. Full-sized bulbs of this kind had been planted on the show grounds of a grower and were harvested but not cleaned. Of these I made a random selection of 40 bulbs which evidently had not lost any offsets. The total harvest of these 40 bulbs consisted of 21 large bulbs (11–12 cm. in circumference), 18 smaller blooming-size bulbs, and 42 ranging below this size to very small. It was interesting to note that 14 had merely replaced themselves, 14 produced two bulbs, nine each three bulbs, and three four bulbs each. The average rate of bulb production, counting all sizes, was slightly over two. This is typical of the early double tulips not only in Michigan, but also under the cultural conditions obtaining in the Netherlands.

In comparison with these figures 21 undisturbed plants which produced some kind of flower averaged 8.14 bulbs and bulblets per plant; the minimum was four, and the maximum, eleven. The total weight of the new bulbs produced by these plants ranged from 21.2 to 48.5 grams, average 35.46 grams. The average weight of 37 normal maximum-size bulbs of Mr. van der Hoeft is 20.4 grams. Our data indicate that parthenocarpy does not interfere with crop production, possibly because of extensive photosynthesis by the carpels. It is generally held that seed production does reduce the bulb crop. Since only three plants yielded seeds, our data are inadequate to justify conclusions on this point.

It is remarkable that plant no. 15 had four bulblets, weighing a total of 7.8 grams in spite of the fact that it never formed roots or developed any leaves. No. 17 grew leaves in the soil, but they never came up. It developed seven bulblets with a total weight of 15 grams. Similarly, no. 19 produced three bulblets, weighing a total of 12.3 grams.

In addition to the accelerated rate of reproduction, departures of the new bulbs from the parent characteristics were also observed. Clone 5 had a markedly rougher and whiter tunic. Clone 30 was so oddly rounded that the bulbs resembled small potatoes, and it was almost impossible to tell the apex from the root crown. Three (nos. 9, 18, and 31) produced one bulb each in the axil of a leaf underground. The last variation also occurs occasionally in normal bulbs. For the convenience of the reader most of the results described are combined in Tables I–IV.

In retrospect it is very clear that an unusual influence has caused many changes which can hardly be explained except on the basis of secondary irradiation from radioactive materials. It must also be remem-

bered that all plants underwent what probably is a temporary stunting effect. This normally disappears after the second crop, at least when X-ray is used (3).

GAMMA EXPERIMENT

If the irradiation of these tulips was due to radioactive chemicals¹ in the bulbs with which they were packed, the influence of beta rays was probably negligible and gamma rays must have been largely responsible. To test this hypothesis a gamma irradiation experiment with the same variety of tulips is now in progress. Twenty bulbs were retained for controls. Forty were exposed to Co⁶⁰, which emitted 10 mc. from a glass vial placed in the center of the tulip bulbs for 28 days.² The nearest tulip bulbs had their centers 1 cm. from the source. In air the available energy at this point was $m\text{r/hr} \frac{5.6 \cdot .01 \cdot 2.4 \cdot 10^6}{1} = 134.4 \text{ r/hr}$ or $28 \times 24 \times$

$134.4 \text{ r} = 89316.8 \text{ r}$ in all. The greatest distance between the source and the center of the bulbs in the periphery was 10 cm. The absorption by the tulip tissues is unknown, but it is probably very high, and it affords considerable protection for all but the nearest tulips.

The glass of the vial probably screened out all beta rays. If it actually did so, the energy emitted should represent pure gamma rays.

The wide variation in the present experiment should be a good approximation of what happened to the lot discussed in this paper. The distance from their source of irradiation must also have varied considerably. Thirty days after exposure all 37 available gamma-irradiated tulips had failed to develop a visible apical bud. Every one of the 20 controls from the same original lot, kept under nearly identical conditions, had made a visible apical growth from a few millimeters to more than one centimeter. Root-crown development was also markedly delayed in the irradiated lot, but much-enlarged root crowns with many individual root tips were the rule in the 20 controls. Since inhibition of growth and root development was characteristic of irradiation effects in the first set of experiments, the author is encouraged to believe that gamma rays were also responsible for the effects on the 30 tulips reported in this paper.³

¹ Primarily sodium (personal conversation with Dr. Norbert J. Scully, of the Argonne National Laboratory).

² Courtesy of Dr. Lester Wolterink, Michigan State College.

³ By July 15, 1950, reduction in the height of the plants, marked development of lateral buds, increased rate of multiplication, increased crop production, and marked parthenocarpny had resulted from the gamma radiation.

SUMMARY

Thirty tulip bulbs which were packed and shipped with 440 neutron-irradiated bulbs afterward underwent marked physiological and morphological modifications. A commercial lot of the same variety, grown 30 feet distant in the same field, under practically identical conditions, was used as controls.

Three tulips failed to come up; three others were used for study. Twenty-four grew 3 to 24 cm. high, average 16.38 cm. Normal plants did not exceed this maximum height, but averaged 20.9 cm. The experimental plants lived about one month longer than the controls. The following departures from normal were observed in their leaves: modified spacing along the stems; failure in development of the distal ends, causing them to be much curled and torn; variegated coloring; upper leaves partly or wholly petal color; splitting of the apices of the leaves for a variable distance; and, in one leaf, a dead brown streak.

Twenty-one plants developed flowers, but all were abnormal. Many petals were badly burned and failed to develop. Instead of the almost uniform yellow color, many were variously marked with red, brown, white, and green, or with a combination of these colors.

Most of the pistils were split, fasciated, bent, or otherwise abnormal. In some, pigmentation was lighter than usual, others were reddish, one had a purplish-blue stigma. In still others the stigma appeared burned. Ten of twenty pistils lived much longer than those of the controls and enlarged markedly. Seven of these produced no seed. The enlargement probably is parthenocarpy due to irradiation effect, but it may be due to pollination of sterilized ovaries. Three plants developed some small seeds, but mostly hulls. Self-fertilization is excluded. Three pistils, including two of the three which produced seeds, developed enlarging ovules on the outside, which colored red.

Forty closely related early double tulips under somewhat more favorable conditions produced a total of 81 bulbs or bulblets, an average of 2.02 bulbs per plant. Twenty-one undisturbed experimental plants each produced four to eleven bulbs or bulblets, an average of 8.14 per plant. The longer photosynthetic period is probably an important contributory factor. Ovarian growth did not appear to interfere with crop production. Bulbs which did not grow, or which developed only underground growth, produced three to seven bulblets. Departure from the normal shape of the bulbs, as well as differences in color and texture of the tunics, occurred.

Since irradiated tulips are most likely to affect others by the gamma

rays which they produce, a control experiment with gamma rays was undertaken. Thus far the same delay in development has been observed as in the recorded experiment, which supports the hypothesis that the effects reported are due to secondary gamma irradiation.

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TABLE I
CULTURAL DATA ON FIVE PLANTS WHICH PRODUCED EXTERNAL OVULES OR SEED

Date of observation, 1949	Place number	Height to pistil tip, cm.	Highest leaves, cm.	Number of leaves above ground	Other modifications	Petals	Pistil on date in Column I	Pistil later	Bulb and bulb-lets harvested 7/6/49 *	Total weight of crop 7/9/49
5/23	2	23	19	5	Leaf 4.5 cm. below ovary, half yellow, like flowers	Yellow and crinkled; had dropped 5/23	Healthy, split on one side; 16 ovules growing to outside of split	6/4: Split deeper, more ovules on outside 6/15: Dried out	11	45
5/27	31	21.5	17	4	Two leaves much split and curled, similar to 23	Dropped	3.5 cm. dark green, bent. Good enlarged ovules on one side; many small ones lower down	6/4: More bent. Swollen on one side. Part with ovules breaking loose	8	37.5
5/27	27	24	16.5	4	Stem not quite straight	Dropped	3.5 cm., 1.8 cm. wide at top; healthy in appearance	6/4: 4 cm. swollen 7/2: Some seed	10	30.7
5/27	28	23	19.5	6	Two upper leaves largely yellow-colored and turgid	Dropped	3.5 cm., broadly fasciated. Stigma 3.7 x 1.5 cm. Healthy, red ovules on both sides	6/4: 4 cm. More ovules showing, much enlarged 7/2: Some seed	7	37
5/23	3	22.7	18	4	.	Dropped	Normal	6/4: 5 cm. swollen 7/2: Some seed	7†	21.2

* One bulblet of 5 grams found loose, cannot be identified.

† Oddly formed.

TABLE II
CULTURAL DATA ON TEN PLANTS OF WHICH THE OVARIES ENLARGED WITHOUT SEED PRODUCTION

Date of observation, 1949	Place number	Height to pistil tip, cm.	Highest leaves, cm.	Number of leaves above ground	Other modifications	Petals	Pistil on date in Column I	Pistil later	Bulb and bulb-lets harvested 7/6/49	Total weight of crop 7/9/49
5/24	13	20	19	4	..	All present. Inner ones scorched. Outer ones turgid, varied colors	Normal	6/4: 3.5 cm., turgid; later dried; no seed	9	44.5
5/24	9	19	19	5	Stem slightly crooked	Mostly present, half dried. Outer green and varied colors	3.5 cm., normal	6/4: Dried	9 *	36.2
5/24	10	21	18.5	4		Dropped	3.5 cm., normal, losing color	6/4: Dried	6	36.3
5/27	30	23	19.5	5	Stem almost erect	Dropped	3.4 cm., green except upper part seems scorched and cleft several times	6/4: Dried	8	37.5
5/27	25	20.5	18	3	Third leaf 5 cm. below pistil has edges reddish and white	Dropped	3.5 cm., normal, growing on one side, drying on the other	6/4: Dried	7	36.3

TABLE II (Continued)
CULTURAL DATA ON TEN PLANTS OF WHICH THE OVARIES ENLARGED WITHOUT SEED PRODUCTION

Date of observation, 1949	Place number	Height to pistil tip, cm.	Highest leaves, cm.	Number of leaves above ground	Other modifications	Petals	Pistil on date in Column I	Pistil later	Bulb and bulb-lets harvested 7/6/49	Total weight of crop 7/8/49
5/23	7	20	19.5	6	One inch stem between each two leaves	Mostly turgid except few central ones to one side. Reddish-brown markings	Light green, turgid	6/4: Dried	9	34.8
5/27	18	21.5	20.5	5	Dropped	3 cm., upper 7 mm. swollen, purplish blue	6/4: Dried	9 *	48.5
5/27	20	19.5	19	5	Stem crooked. One leaf with dead brown streak through center. Leaf half yellow and half red	Dropped	Reddish, narrow, spreading; stigma dried out	6/4: Dried	9	39.5
5/24	11	22.5	17.5	3	Basal leaf very wavy at edge. Plant at 80° angle. Leaves darker green than those of other tulips	Dropped	Normal, 3 cm. drying	6/4: Dried	4	34.9
5/27	26	20	15	4	Dropped	3 cm., drying stigma, deeply divided	6/4: Dried	9	31.5

* One bulb one inch above the others.

TABLE III
CULTURAL DATA ON SIX PLANTS OF WHICH THE PISTILS WITHERED WITH THE FLOWERS

Date of observation, 1949	Place number	Height to pistil tip, cm.	Highest leaves, cm.	Number of leaves above ground	Other modifications	Petals	Pistil on date in Column I	Bulb and bulb-lets harvested 7/6/49	Total weight of crop 7/9/49
5/27	21	15.5	17	3	Stem crooked	Poor; distal parts dried	2 cm. long, dried	9	25.5
5/27	22	14.5	14	6	Upper leaf fused in part with stem. One inch edge white and pink	All dried. One petal 8 mm. below flower	2 cm., dried	8	26.3
5/24	12	19	20.5	4	One quarter present. Varied colors	Dried out	9	47.7
5/27	23	11.5	11	4	All upper edges much curled and torn in appearance	Dried flower bud	Dried flower bud	6	38.5
5/23	5	18	17	6	One left	Dying, split two fifths of length	7 *	29.3
5/23	6	18	17	6	Grows at angle of 15° from vertical. One split leaf	One greenish. Several dried	Dying	10 †	26

* Whiter, rougher tunic.

† One bulb one inch above the others

TABLE IV
CULTURAL DATA ON NINE PLANTS WHICH DID NOT BLOOM, DID NOT COME UP, OR
WERE DISTURBED DURING THE GROWING PERIOD

Date of observation, 1949	Place number	Highest leaves, cm	Number of leaves above ground	Remarks	Bulb and bulbets harvested 7/6/49	Total weight of crop 7/9/49
5/23	4	5.5	2	Roots not investigated	1	5.8
5/24	14	3	2	Roots not investigated	5	23
5/27	17	0	0	Turgid leaves curled in soil. Tip of internal bud showing above bulb. Dug away 2 1/2" of soil to give it a chance	7	15
5/27	19	0	0	2 1/2" growth above bulb. Dug away 2" of soil to give it a chance	3	12.3
5/25	15	0	0	Shoot 1 3/4", two internal buds 3/4" and 1" above bulb. No roots. Replaced 2" deep	4*	7.8
5/27	24	0	0	Internal bud 2 cm. above bulb. Stem and leaves used for study. Covered and left; roots not investigated	8	17.7
5/27	29	0	0	Stem broken off; internal bud 1 1/4" above bulb. Replanted after earlier inspection. Bulb 3" deep	5	11.5
5/24	16	12.5	4	Dried up. Was dug up for root collection May 20	6	18.5
5/27	32	0	0	Dried up, used before for roots	6	22.4

* One of the four was partly eaten.

FORESTRY

SOME RESUPINATE POLYPORES FROM THE REGION OF THE GREAT LAKES. XXII*

DOW V. BAXTER

THIS series of papers (2) is offered as a conservative summary of our knowledge of the taxonomy of the resupinate polypores of North America, their occurrence and natural and artificial ranges, the hosts and the substrata attacked, their reaction in culture, and their importance. In this collection of widely distributed species that belong to several genera a large amount of variation is to be expected. Several plants described become resupinate only under certain conditions, but these species are included, in this series, not only because of the taxonomic problems they create, but also because of the possible economic significance of some of them when growing in artificially created environments.

This paper emphasizes certain unusual environments, host, and substrata for some of the common members of the group and presents descriptions of *Lenzites saepiaria* and *Polyporus licnoides*.

The color terms given within quotation marks are those of R. Ridgway, *Color Standards and Color Nomenclature* (Washington, 1912).

Polyporus licnoides Mont., Pl. Cell. Cuba 401. 1842

Polystictus licnoides Fr., Nov. Symb., 92. 1851.

Polystictus subglaber Ellis and Macbr., Bull. Lab. Nat. Hist. Univ. Iowa, 3: 192. 1896.

*Throughout the work on these monographs (2) I have been indebted to many individuals and institutions for suggestions, help, and privileges extended to me. Grants from the Horace H. Rackham School of Graduate Studies of the University of Michigan have greatly facilitated both the field and the laboratory studies. My appreciation is expressed particularly to the men who have accompanied me on my numerous expeditions to Alaska, the Yukon Territory, the Northwest Territories, Newfoundland, and Labrador. Much credit is due them for aiding in the collection and care of specimens and for living, at times, under rather difficult circumstances. I am under obligation to Professor T. G. Halle, of Naturhistoriska Riksmuséet in Stockholm, with whom I have had the pleasure of association. Thanks are also due to several American institutions and scholars. To the authorities at the New York Botanical Garden, to the staff of the Division of Pathological and Mycological Collections of the United States Department of Agriculture, and to the Division of Botany, Central Experimental Farms, Ottawa, Canada, I am especially indebted.

Hapalopilus licnoides (Mont.) Murr., Bull. Torrey Bot. Club, 31: 417. 1904.
Polyporus subtropicalis Spegazzini ex Lloyd (*The Genus Polyporus*, p. 387. 1915);
Polyporus xerophyllaceus Berk., Hook. Journ. Bot., 8: 200. 1856; ex Romell in
Murr., Bull. Torrey Bot. Club, 31: 417. 1904.

Fructification on wood of southern hardwood trees, thin, coriaceous, imbricate, aplanate, or sometimes resupinate; surface multizonate, concentrically striate, finely tomentose to subglabrous, subshining, brown with buff zones, "tawny olive," "cinnamon," "army brown" to "bister," and typically with smooth brownish-red areas on the pileus; context thin (1 mm.); tubes short, 1–2 mm.; spores ellipsoid or subglobose, hyaline $3-4 \times 2-3$ (Murr.); setae brown.

Allied species.—This plant, common in subtropical parts of Florida and elsewhere in America, is closely allied to *Polyporus gilvus*. It may with reason be considered a thin form of *Pol. gilvus*, but the name has become so well established that it seems best to retain it. Although certain growth forms of *Pol. licnoides* and *Pol. gilvus* appear to be nearly alike, the two plants are ordinarily distinguished by the numerous concentric zones which ornament the surface of *Pol. licnoides*. The context is usually rigid in *Pol. gilvus*, whereas that of *Pol. licnoides* is ordinarily more flexible (17). In typical specimens of *Pol. licnoides* smooth reddish areas occur on the fructification to a greater extent than in most specimens of *Pol. gilvus*. The pileus in *Pol. licnoides* is much more zonate.

Because of some similarity in their specific epithets *Polyporus lignosus* Klotzsch might be confused with *Pol. licnoides*, but its color and its conspicuously multizonate pileus differentiate it from *Pol. gilvus*.

Since *Poria rufitincta* Cooke sensu Murrill is both thin and ferruginous and assumes a brown-reddish tinge, it might be mistaken for a resupinate specimen of *Polyporus licnoides*. Furthermore, the mouths of both plants are small, i.e. mostly seven to a mm., and both have setae. However, the spores are ellipsoid to subglobose and measure $3-4 \times 2-3 \mu$ (Murrill) in *Pol. licnoides* and are subglobose and larger and measure $4-5 \mu$ in *P. rufitincta*. *Pol. licnoides* early exhibits a reflexed habit of growth, so that care should be taken in the field to collect material which shows this tendency. *P. rufitincta* cracks somewhat upon drying, a feature which is only relative, but one not so likely to occur in *Pol. licnoides*.

Polyporus extensus is another tropical plant which might be confused with *Pol. licnoides*, but it usually has stratified tube layers and is ordinarily a thicker plant than *Pol. licnoides*. The spores of *Pol.*

extensus are described as fulvous, whereas those of *Pol. licnoides* are hyaline.

Fomes conchatus, in a resupinate state, may also bear some resemblance to *Polyporus licnoides*, but it, too, is a much thicker plant and ordinarily exhibits the stratified tube layers. The plant determined as *F. Ribis*, a very close relative of *F. conchatus*, has been confused with *Pol. licnoides*. Setae are abundant in *Pol. licnoides*, whereas *F. Ribis* has no setae.

Habitat.—*Laurocerasus caroliniana*, *Liquidambar Styraciflua*, *Magnolia grandiflora*, *Melia azedarach*, *Myrica cerifera*, *Persea Borbonia*, *P. palustris*, *Prosopis juliflora*, *Quercus Michauxii*, *Q. virginiana*, *Sapindus marginata*, *Sassafras* sp., *Torreya taxifolia*.

Distribution.—Florida, Louisiana, Mississippi, Missouri, South Carolina, Tennessee, Texas.

Occurrence.—*Polyporus licnoides* occurs in North America most generally in the southern United States, but elsewhere it appears more widely; in semitropical and tropical areas. It is known from Argentina, Brazil, British Guiana, British Honduras, Colombia, Costa Rica, Cuba, Dutch East Indies, Guatemala, Haiti, Jamaica, Mexico, New South Wales, Nicaragua, Panama, Peru, Philippine Islands, Venezuela, and Virgin Islands.

Lenzites saepiaria (Wulf.) Fr., Ep. 407. 1838

Agaricus hirsutus Schaeffer, Fung. Bavar., 4: 33, pl. 76. 1762. Teste Murrill, 1908.

Agaricus saepiarius Wulfen in Jacq. Coll., 1: 347. 1786.

Agaricus boletiformis Sowerby, Engl. Fungi, pl. 418. 1814. Teste Murrill, 1908.

Daedalea saepiaria (Wulf.) Fr., Syst. Myc., 1: 333. 1821. Fries, Obs. Myc., 1-105. 1815. Teste Murrill, 1908.

Gloeophyllum saepiariarium (Wulf.) Karst., Karsten, Hattsv., 2: 80. 1882.

Gloeophyllum hirsutum (Schaeff.) Murr., Journ. Myc., 9: 94. 1903.

Gloeophyllum abietinellum Murrill, North Am. Fl., 9: 129. 1908.

Lenzites rhabarbarina Berkeley et Curtis, Ann. Mag. Nat. Hist., II. 12: 428. 1858. Teste Murrill, 1908.

Lenzites saepiaria porosa Pk. ex Lowe, Pol. New York, 108. 1927.

Sesia hirsuta (Schaeff.) Murr., Journ. Mycol., 9: 88. 1903.

Fructification coriaceous, sessile, dimidiate, effused-reflexed or sometimes resupinate; 1-4 × 9-10 × 0.5-1 cm., surface "argus brown," "bone brown," grayish black on weathering, surface anoderm, tomentose, or strigose, smooth or slightly tubercular, zonate, margin rather thick, nearly entire; context soft, punky, homogenous, yellowish brown, "ochraceous tawny" or "argus brown" in old plants, 1-3 mm. thick; usually lamellate below, anastomosing at first, "light ochraceous buff"

to "ochraceous orange" or grayish, in poroid forms tubes circular, 1–2, mostly 2, to a mm., edges thick, entire; basidia $4.5\text{--}6 \times 18\text{--}30 \mu$ (Pilát); spores hyaline, cylindrical, $3\text{--}4.5 \times 7\text{--}12 \mu$,¹ without conspicuous cystidia, sometimes with cystidioles (hypha-like with encrusted ends) $4\text{--}6 \mu$ in diameter.

Allied species.—A closely related polypore to *Lenzites saepiarina* is *Trametes odorata* (Wulf.) Fr. Emphasis was once given to the suggestion that they were identical because of the occasional occurrence of the two growing near together or even on the same piece of wood. Furthermore, the hymenium of *Lenzites saepiarina* is often so variable that there is reason for confusing the species (Pl. I). It may be lamellate, daedaloid, or somewhat poroid or irpiciform if growing on unusually wet wood (25).

The difference in the temperature reactions of the two organisms in culture supports the now accepted view that *Trametes odorata* is a species distinct from *Lenzites saepiarina*. A test of growth upon a single agar at temperatures from 30° to 36° C. would serve to distinguish the fungi in culture.

In tests made on cultures of the two fungi (26) there is no apparent difference in the optima of the two species. *Trametes odorata*, like *Lenzites saepiarina*, has an optimum temperature—between 30° and 34° C. Their upper limits of growth are, however, different. *L. saepiarina* is not inhibited until after 40° C. is reached, whereas *T. odorata* was only barely growing at 38° C. and would not develop at all at 40° C. Furthermore, the rates of growth of the two organisms differ. *L. saepiarina* grows faster at all temperatures, the rate being more pronounced between 28° and 30° C.

Their odors may usually be used to separate *Lenzites saepiarina* in cultures from the related *Trametes odorata*, which has a distinct aromatic odor like fennel, whereas *L. saepiarina* does not usually have an odor.

Among the noteworthy microscopic features of the mycelium "medallions" should be mentioned. Apparently they are observed only on wood and not in artificial culture.

The European *Lenzites abietina* is closely related, but Shope (23)

¹ Snell (25) reports that spores from fruiting bodies that appear on roof timbers inside cotton mills are "often smaller than those from fruit bodies collected out of doors. They have been found to measure $6\text{--}9 \times 2.5\text{--}3 \mu$ (mostly $6\text{--}7 \times 3 \mu$), whereas $8\text{--}12 \times 2.5\text{--}4 \mu$ are reported measurements given by most mycologists."

separates these two fungi on the basis of the presence of ventricose cystidia in the latter.

Habitat.—*Abies amabilis*, *A. balsamea*, *A. concolor*, *A. Fraseri*, *A. grandis*, *A. lasiocarpa*, *A. magnifica shastensis*, *Acer pennsylvanicum*, *A. rubrum*, *Alnus tenuifolia*, *Arbutus Menziesii*, *Betula lutea*, *B. papyrifera*, *B. papyrifera occidentalis*, *Chamaecyparis nootkatensis*, *C. thyoides*, *Cupressus guadaloupensis*, *C. macrocarpa*, *Fraxinus americana*, *Juniperus pachyphloea*, *Larix europea*, *L. laricina*, *L. leptolepis*, *L. occidentalis*, *Picea Engelmannii*, *P. excelsa*, *P. glauca*, *P. mariana*, *P. pungens*, *P. rubra*, *P. sitchensis*, *Pinus Banksiana*, *P. contorta*, *P. echinata*, *P. glabra*, *P. Lambertiana*, *P. laricio* (Corsican), *P. monticola*, *P. Murrayana*, *P. palustris*, *P. ponderosa*, *P. resinosa*, *P. rigida*, *P. Strobilus*, *P. sylvestris*, *P. taeda*, *P. virginiana*, *Populus tremuloides*, *Prunus pennsylvanica*, *Pseudotsuga taxifolia*, *Salix discolor*, *Sequoia sempervirens*, *Taxodium distichum*, *Thuja occidentalis*, *T. plicata*, *Tsuga canadensis*, *T. heterophylla*, *T. Mertensiana*.

Distribution.—Alaska, Northwest Territories, Yukon Territory; Alberta, British Columbia, Labrador, Manitoba, New Brunswick, Newfoundland, Nova Scotia, Ontario, Prince Edward Island, Quebec, Saskatchewan; Alabama, Arizona, Arkansas, California, Colorado, Connecticut, Delaware, District of Columbia, Florida, Georgia, Idaho, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Montana, Nebraska, New Hampshire, New Jersey, New Mexico, New York, North Carolina, North Dakota, Ohio, Oregon, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Texas, Vermont, Virginia, Washington, West Virginia, Wisconsin, Wyoming.

Occurrence.—*Lenzites saepiarum*, one of the most abundant fungi on dead coniferous timber in North America, is worldwide in its distribution. It is not nearly so common a cause of decay of softwood in Great Britain as on the continent of Europe and in North America (9).

The fungus causes extensive damage by its occurrence on exposed timber in service, especially poles, posts, and ties. It is known on hardwoods (Pl. II), but it is a much more common destroyer of coniferous slash. Wet environments and long exposure in such places are particularly important factors influencing the abundance of the fungus. For example, after a storm of extraordinary violence in the Olympic Peninsula, Washington, *Lenzites saepiarum* occurred abundantly on western hemlock, *Tsuga heterophylla*, a species that con-

stitutes a large part of the volume of overmature West Coast timber. It appeared sparingly, however, on silver fir, *Abies amabilis*, and no decay was attributed to the fungus in western red cedar, *Thuja plicata*. The small amount of rot attributed to this fungus in other timbers was slight in comparison with that caused by *Ganoderma* (*Fomes*) *applanatum* and *Fomes pinicola* (5). All the woods are given in this series or substrata for *L. saepiarum*. On the other hand, fruiting bodies may develop under favorable conditions and have been known to form in green timber within five months (5). In general, its occurrence in standing living timber has been either overlooked or reported as rare (4).

Its significance as a possible agent of destruction of living trees has been underestimated, chiefly because there are few environments that promote its occurrence in standing timber.

Forest practices in the plantations of jack pine, *Pinus divaricata*, on the Nebraska National Forest have resulted in conditions that favor development of *Lenzites saepiarum* (Pl. III). Severe sunscald injury has resulted because of pruning (see section "Decay in Living Trees").

Cultures.—Isolated from *Picea mariana*, Ann Arbor, Michigan; from *Picea mariana*, Goose Bay, Labrador; Central Experimental Farm 17246); from *Betula alba papyrifera*, Goose Bay, Labrador; Central Experimental Farm, Ottawa (17240).

Lenzites saepiarum exhibits so much variability even within the same isolate that variability appears to be a feature that must be considered in the diagnoses of cultures. Cultures often show a mat ranging from a white more or less even-granular or powdery surface to one that is irregularly tufted with thick cushions of brown cottony mycelium. Most cultures develop this tufted growth in age. Snell (23) points out that cultures can be readily distinguished by the scant superficial mycelium and by the powdery appearance given by the oidia. In seven days a mat with a radius of 20 mm. is produced. In fourteen days a mat with a radius of 41 mm. or more develops; it is velvety, "ochraceous orange," "raw sienna," or "amber brown" and has "maize yellow" margins.

The allied *Lenzites trabea* exhibits a paler brown ("orange buff" or "ochraceous salmon") mycelium than that produced by *Lenzites saepiarum*.

Fructification in culture.—Two general types of fructification may

form in malt-extract cultures: (a) basidia, which may grow directly on the mycelium, and (b), after a minimum of about three weeks' growth, white cushions, which are composed of aerial mycelium. Some of these formations may appear slightly stipitate. They gradually change color, passing through various shades of yellow and finally are "cinnamon" to "Prout's brown." This form of fructification is said by Cartwright (7) to suggest the general form of a Sparassis, with bifurcating tips, but the tips may be branched or unbranched. Individual segments may be flattened, although not to such an extent as to approach lamellae in appearance.

In the less specialized type of fructification slightly raised cushions may appear scattered over the surface of the culture, or they may be widely effused and scarcely raised above the level of the surrounding mycelium. These cushions are "capucine yellow," "cinnamon rufous," "russet brown," or "mikado brown." The hymenial layer occurs over the surface, and basidia often appear directly on the mycelium, apparently with no specialized hymenial layer, as in the genus *Hypochnus*.

The basidiospores produced are viable. Cartwright (7) finds they are usually shorter than those borne on normal fruit bodies, but are otherwise similar. The spores are cylindrical and curved, and measure 6-8 \times 3-3.5 μ . Secondary spores may also develop in culture. Chlamydospores are formed on the submerged mycelium, and on the aerial mycelium pear-shaped oidia develop.

Cultures of *Lenzites saepiaria* resembling somewhat those of *Trametes odorata* often produce a mat of sodden appearance with no trace of aerial growth. When aerial growth does develop, it is mostly as secondary mycelium. This is characterized by the rich production of oidia, which lend to it a more or less powdery appearance (24).

The tertiary mycelium, which in color and texture resembles the tramal tissues of the sporophores, is often arranged in radiating rows, frequently merging together to form longer ridges, or wider cushions, or mats (24, 18).

Cultures usually stain the agar dark red brown, though not always. The agar stain seems, however, to be the only character which is approximately constant within the same isolation (22).

Fructifications (isolate from *Picea mariana*, Labrador) have appeared in the Michigan wood-block cultures of both red gum (*Liqui-*

dambar Styraciflua) and white pine (*Pinus Strobus*) in one-year-old tests. These appear much like a minute *Sparassis* as described by Cartwright and Findlay (8). No fructifications have appeared on either red-gum or white-pine blocks in two-year-old tests made with the isolate from birch.

The highest growth rates have been observed by Robak (22) on malt and potato-dextrose agars, and the rate was decidedly slower on xylose than on the other sugars tested. Development on media containing nitrogen of different types is variable, except that the growth is slow on NH_4NO_3 and $(\text{NH}_4)_2\text{SO}_4$.

The temperature for optimum growth of *Lenzites saepiaria* on a number of isolates has been tested by different investigators. Snell and his collaborators (26) note that the optimal range of the isolates they used was between 30° and 34° C., the best growth occurring perhaps at 32° C. Humphrey and Siggers (13) obtained satisfactory growth from 30° to 36° C.; the highest growth rate was at 36° C. (These authors used a medium which contained beef extract in addition to malt.) Robak (22) found that in five Norwegian and two Canadian isolates the best growth was obtained at 32° C., and that at 30° C. the development was only slightly slower, results which conform well with the observations made by Snell and his collaborators. At 35° C. growth was retarded, and it was checked at 38° C. in four isolates, including the two from Canada. Snell, Hutchinson, and Newton (26) observed a growth at 38° C., which was about half as rapid as the optimal one, whereas at 40° C. the growth rate appeared to be about the same as that observed at 38° C. Growth was not stopped until a temperature of 43° C. was reached. Robak (22) calls attention to the fact that the diverging results should be interpreted as due to differences in temperature resistance within the individual strains. The two Canadian cultures of the isolates he tested belong to the least resistant strains.

Snell (25) found that an exposure of three and one-half days to 44° C. or of twelve hours to 55° C. under moist conditions was necessary to kill *Lenzites saepiaria* growing on small blocks of Sitka spruce, whereas with dry heat the temperatures necessary to kill in three days were from 70° to 90° C.

Microscopical appearance in culture.—The submerged hyphae are colorless, thin-walled, abundantly septated, seldom branched, and almost always without clamp connections; they measure 1.5–5.1 μ , being

mostly about $3\ \mu$ in width. Oidia or chlamydospores sometimes present. Aerial mycelium colorless, branched, soon breaking up into oidia. Clamps sometimes present. Oidia colorless, mostly ellipsoid, ovoid to globose or pyriform, more rarely cylindrical, measuring $4\text{--}35 \times 2.5\text{--}3\ \mu$ (22, 24).

The tertiary mycelium between each two septa is long, stiff, sparingly branched and septate, most often with a clamp connection, more or less approaching the medallion type found in decayed wood (22).

Robak (21) reports that on gallic-acid media there was seldom any oxidase reaction and that it was often late in occurring. Sometimes it was weak, and only rarely was it very strong. There was no reaction on tannic acid. No discoloration of aniline blue was noticed by Robak.

Spore germination.---Basidiospores germinate readily in one or two days in nutrient agar and even in tap water. Snell (24) reports that diffuse light had no effect upon germination, but most of the spores were killed upon exposure to direct sunlight for three days. He states that basidiospores do retain their viability under dry conditions for long periods; 25 per cent germinated after storage for two years and ten months.

Decay in culture.---Robak (21) found that *Lenzites saepiaria*, when cultivated on chip material and blocks of pine and spruce, sap and heartwood, and on sawdust of spruce sapwood, causes reductions in dry weight approximating that produced by *Trametes sciralis* and *T. odorata* (22). According to expectation, large losses in cellulose were caused by this brown rot fungus. However, considerable decomposition of the lignin also took place in advanced stages of decay.

The fungus can cause as much as 20 per cent loss in weight in small blocks of pine sapwood after about four months' exposure at 22°C . (8).

Sexuality as exhibited by cultures.---*Lenzites saepiaria* is a heterothallic species (21). Bipolar segregation has been noted by Fries (12). Results obtained by Mounce and Macrae (16) in Canada likewise show that complete interfertility exists between haploid mycelia derived from different sources. In one experiment Robak (21) reports that seventy-nine of eighty-four pairings he arranged exhibited clamp connections. The negatively resulting pairings occurred when one strain or the two combined had been kept in culture for a long time.

Robak (21) investigated Canadian and Norwegian strains and

found them mutually fertile. The interfertility was not absolute, however; the ages of the cultures were given as a possible explanation for this.

Reaction to chemicals.—Extracts from wood have been studied with reference to their toxicity to *Lenzites saepiaria*. Extracts of *Pinus ponderosa* were tested, for example, by Anderson (1). He did not find the extract from the heartwood to be much more toxic than that from the sapwood. Resistance to sodium fluoride was tested by Richards (20), who has arranged a number of wood-destroying fungi according to their reaction to this chemical, beginning with the most susceptible: *Poria incrassata*, *Polyporus abietinus*, *Pol. versicolor*, *Fomes roseus*, *F. pinicola*, *F. subroscia*, *L. saepiaria*, *Pol. hirsutus*, *F. Pini Abietis*, *F. annosus*, and *L. trabea*. The position of *L. saepiaria* is seventh in this list of eleven fungi.

Carswell and Nason (6), who studied the toxicity of other phenols to *Lenzites saepiaria*, report the amounts causing total inhibition of growth as well as death (Table I).

TABLE I

TOXICITY OF SUBSTITUTED PHENOLS TO LENZITES SAEPIARIA

The figures give the percentages of the chemical in the medium.

Causing total inhibition of growth				Causing death			
Penta-chloro-phenol	Sodium penta-chloro-phenate	<i>B</i> naph-thol	<i>p</i> -chloro- <i>m</i> -cresol	Penta-chloro-phenol	Sodium penta-chloro-phenate	<i>B</i> naph-thol	<i>p</i> -chloro- <i>m</i> -cresol
0.002	0.002	0.01	0.01	0.006	0.004	0.05	0.04

Decay: Gross features.—The first indications of rot caused by *Lenzites saepiaria* is a pale-yellow discoloration, accompanied by brittleness and softening, especially in the springwood. Later the wood becomes brown and breaks into cubes by cracking along and across the grain. Little or no superficial mycelium is visible. It has been pointed out by Cartwright and Findlay (9) that, when a cross section of an infected beam is viewed, isolated patches of dark reddish-brown areas may be seen and that, when the decay is more advanced, the cubical rot becomes evident owing to the formation of checks and the separa-

tion of the annual rings. As they state, "Decay is usually confined to the interior of a beam, which may become completely rotted away internally, but yet continue to have a more or less unaltered skin."

Microscopic features.—Only one or two hyphae are usually present in each tracheid, according to Falck (11). He therefore concluded that the hyphae may affect the cell walls for some distance. The hyphae in the wood exhibit many medallions. Yellow mycelium with thickened clamp connections is present in the tracheids beneath fruiting bodies.

Spaulding (27) observed few boreholes, and reported that the hyphae usually pass through the pits.

Decay in living trees.—If certain unusual environments are established that especially favor the development of fungi characteristically on wood products, they will attack living standing timber. *Lenzites sacpiaria* was discovered in 1949 to be at least one cause for decay in standing green jack pine in the extensive and historical plantations on the Nebraska National Forest (Pl. IV). Similar injury has been observed in shelterbelt plantings in the area. The rot is the indirect result of pruning operations, but instead of occurring at the cutting wounds, it became evident initially at the extensive sunscald areas resulting as an aftermath of pruning (Pl. V).

It is apparent that the decay will finally lead to the total destruction of many of the jack-pine stands. The pruned pines exposed to the sun at the borders of the plantations show sunscald injury to approximately the height on the trunk at which the branches were removed. *Lenzites sacpiaria* has been found to infect these trees, and the resulting rot weakens the pine, so that they break during storms (Pl. VI). The nearest adjoining rows then become damaged because of sunscald and rot (Fig. 1). Jack pines not pruned are not damaged, as were those trees with the branches removed (Pl. VII).

Plantings of *Pinus ponderosa* are protected from sunscald by their relatively thick bark (Pl. VIII). *Lenzites sacpiaria* has not infected these trees through pruning wounds.

Enzymes.—Enzyme production for *Lenzites sacpiaria* has been investigated by Zeller (28, 29). The following enzymes have been recorded: esterases, maltase, invertase, raffinase, emulsin, tannase, diastase, hemicellulase, cellulase, pectinase, inulinase, urease, hippuricase, nuclease, protease, erepsin, trypsin, rennet, catalase, tyrosinase.

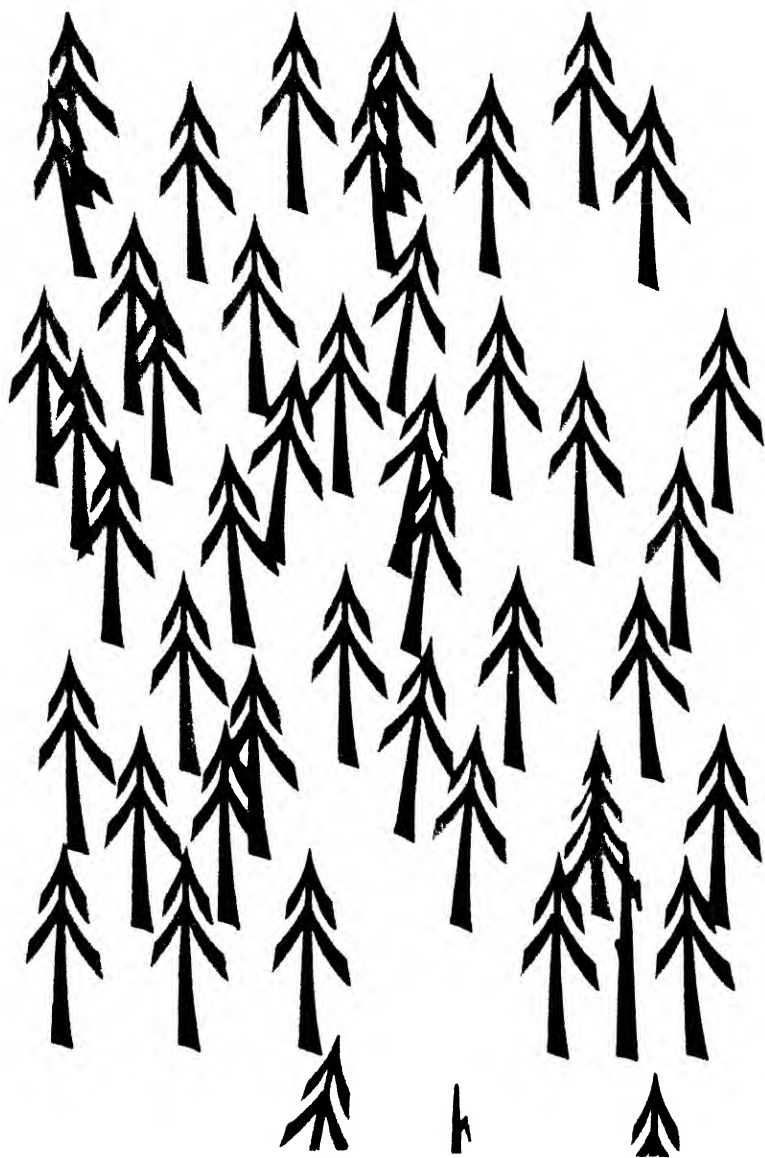


FIG. 1. Sample occurrence of sunscald injury in pruned and thinned jack-pine plantation, Nebraska National Forest. The black parts of trunks define the relative extent of wounds (July, 1949). A dead tree is indicated in black. The rot appears at the sunscald instead of at the pruning wound. The weakened trees blow over, so that protected rows of pine are damaged in turn

and, to some extent, oxidase. Except for the last three enzymes, a greater amount of the enzymes was present in the vegetative tissue than in that of the fruiting body.

Resistance.—It is to be expected that the fungi which are resistant to high temperatures in agar cultures will be among the most resistant to them in wood. It will take longer to kill the fungi in wood, particularly if the wood is dry, than to kill those in agar cultures. Snell (24), using $\frac{3}{4}$ -inch blocks artificially inoculated with *Lenzites trabea*, found that the fungus (together with others tested) was able to withstand 131° F. (55° C.) for twelve hours at moist heat, whereas it took 221° F. (105° C.) for twelve hours to kill all the fungi with dry heat.

Lenzites saepiaria in wood is one of the most resistant to heat. Montgomery (15) found that it was still alive after two hours at 60° C. in wood with an average moisture content of 63 per cent, but that it was killed after two and one-half hours' exposure to these conditions. These results correspond to those obtained by Chidester (10), who reports that the fungus was killed in moist heat maintained at a temperature of 150° F. (65.5° C.) for about one hour.

Prevention and Control.—Storage of pole, tie, and structural timbers must be off the ground and under conditions which provide ventilation. It is necessary to keep the yards free of debris and weeds which hinder air circulation. The time required to season poles (and other products) varies regionally.

Since *Lenzites saepiaria* is one of the common causes of rot in poles in place, several methods have been employed to treat such timbers; among them are the Cobra process and the Pfister methods. The soil is dug away from the poles and a paste preservative is injected at short intervals over an area above and below the ground line. The two processes are much alike, and differ chiefly in details of the construction and operation of the tools. Other processes provide for coatings of various types. Treated sections may be wrapped with building paper to prevent animals from being poisoned by the preservative.

Because it is difficult to obtain a continuous surface of charcoal around the pole and to prevent charcoal itself from breaking away, charring the poles at the surface of the ground is seldom practiced. Furthermore, *Lenzites saepiaria* can readily infect the charred pole through checks. Charring is sometimes used before standing poles are sprayed with a preservative.

Various types of treatment of poles, posts, and other timbers to prevent decay have been discussed elsewhere (3).

For thin-barked trees planted on sites subject to high temperatures, pruning should be avoided; at least on the rows of trees that are exposed to the sun at the margins of the plantation. Thinning practices should likewise be avoided at the borders of the forest. Jack pine grown on such sites is ordinarily best suited for fence-post timbers. The trees cut for posts may be limbed at the time of felling. In general, thick-barked trees such as ponderosa pine are not subject to sunscald. Juniper, although easily broken by winter storms, has not been damaged by sunscald in the plantings observed. Mixtures containing juniper may be used for such areas. Interplanting with either *Juniperus virginiana* or *J. scopulorum* in the more open stands subject to sunscald is urgently recommended.

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PLATES I-VIII



Intermediate forms of *Lenzites saccharia* and *Trametes odorata* may be distinguished in culture more satisfactorily than by morphological features. This form even suggests *T. carbonaria*. Substratum white spruce. Moose Pass, Alaska



Lenzites saccharia on white birch. Goose Bay, Labrador



Sunscald in jack pine plantation established in 1911. This stand was pruned and thinned. Nebraska National Forest. Photograph made in 1940



Fruiting body of *Lenzites saepepila* at sunscald wound of pruned jack pine.
Nebraska National Forest



Sunscauld injury in jack pine at margin of plantation, Nebraska National Forest
Note the severity of the wounds, which extend to the approximate height
of the pruning



Effects of *Lenzites saccharina* in jack pine on trees at margin of plantation, Halsey, Nebraska. The fungus infected the trees, not at the pruning wounds, but at the sunscald injuries resulting from the operation. Destruction of the trees is inevitable



Pruned and thinned jack pine (left) and unpruned and unthinned stand (right). Sunscald injury appears in the pruned and thinned part of the stand



Ponderosa pine, pruned but not injured by sunscald because of the thick bark.
No decay appears in these plantings

RECENT FOREST TAX LEGISLATION IN NEW HAMPSHIRE

J. WILLCOX BROWN

SITUATED between Maine and Vermont, New Hampshire comes naturally by its reputation as one of our more conservative states. In spite of the traditionally cautious approach of its people to any new tax measure, in 1949 the state legislature agreed to as comprehensive a substitution of the yield tax for the property tax on timber as has been attempted in any other state. In addition, a forest-conservation inducement was coupled with the yield-tax venture.

THE YIELD TAX IN THEORY AND PRACTICE

The theoretical imperfections of the yield tax as a revenue source alternative to the general property tax were highlighted in the report *Forest Taxation in the United States* (2), by Professor F. R. Fairchild and associates. On a nationwide scale, the primary importance of lightening the property-tax load through increasing the efficiency of local government was emphasized. Next, the investigators pointed out the importance of sounder administration and of more thorough collection of the property tax in the interest of all property owners. Finally, they admitted the unique handicap under which deferred-yield property labored, but declared that the yield tax was an inadequate solution because it imperiled the fiscal foundation of local government. While placing the position of deferred-yield properties in proper perspective as third in importance of the major deterrents to better forest practice, the taxation experts offered three alternative approaches to the yield tax as a solution. Of these proposed alternatives it is sufficient to say that none of them has received widespread support for enactment into law in any state. The yield tax, on the other hand, usually has been retained in those states where it existed in one form or another and repeatedly has been the basis for proposed legislation.

Opposition to the yield tax on practical as well as on theoretical grounds has caused modifications in it for the sake of expediency in those

places where it has been applied. For the most part yield-tax laws have been optional. Actually, very few timberland owners have classified their lands under the yield-tax provision in any state having the necessary optional legislation, such as Michigan or New Hampshire. In almost every case the yield-tax principle has been modified, so that a separate annual property tax is retained on the land, with the timber being subjected to a yield tax at the time of harvest. In several states the full property tax has been retained, but a severance tax at the time of harvest has been superimposed. In Oregon and Washington substitution of the combined land and yield tax for the property tax has been restricted to cutover lands. Before 1949 Mississippi was the only state in which the property tax on standing timber had been uniformly replaced by a yield tax. It imposes the yield tax at the nominal rate of 3 per cent.

THE SITUATION IN NEW HAMPSHIRE BEFORE PASSAGE OF THE NEW LAW

Against a background of nationwide caution in application of the yield-tax principle, New Hampshire's recent tax venture is not easy to understand. Forest land, covering about 84 per cent of the area of the state, is its major natural resource. Realization of the significance of the forest resource undoubtedly was a factor in the change, but a comparable situation in certain other states has not yet prompted similar action in them.

The local tax picture that existed in New Hampshire prior to the passage of the new law shows more clearly the reasons for action. The tax base is notoriously narrow, having strict limits imposed by meager natural resources. Other restrictions have been added either by the state constitution or by legislative reluctance to supplement the general property tax with newer types of taxes. The tax burden, on the other hand, is inevitably high because of a diverse settlement pattern in rough mountainous country, with correspondingly high costs for provision of public services.

This diverse settlement pattern is perpetuated through the structure of local government. The state has a land area of 9,302 square miles, amounting to a little less than 6 million acres. This area is divided into 234 organized towns and cities, with 22 additional "unincorporated places" in the more isolated mountainous localities. These 256 units are in turn grouped into ten counties. It is in the New England towns that

our purest form of democracy persists, being displayed annually at the March town meetings.

From various sources I have estimated that total revenues of about 25 million dollars were necessary to meet local governmental expenses in New Hampshire in 1945-46 (1). The general property tax was the major single source of local revenue, totaling roughly 19 million dollars. Thus slightly more than 75 per cent of the local tax burden was resting on the general property tax. Miscellaneous local sources accounted for an additional 18 per cent of the local revenues. The state-assessed taxes distributed to the towns, including the railroad tax, savings bank and building and loan tax, insurance tax, and the interest and dividends tax, provided slightly less than 4 per cent of the total local revenue. Essentially these are taxes on intangible property, collection of which has been shifted from the towns to the state. It is significant that less than 3 per cent of the total local revenues apparently was provided through other state and federal payments and grants. This situation is a far cry from Michigan's sales-tax diversion.

The total property tax per acre offers an additional means of comparing the property-tax burden in New Hampshire with the situation in Michigan. In the absence of any recent published statement of the amount of the property tax per acre on rural New Hampshire land, I have endeavored to compute a per acre tax on rural values from the State Tax Commission reports (1, 4). The result obtained has necessarily been an approximate one. The taxes for the eighteen towns and cities classed by the census as urban were completely excluded from the state totals. The tax attributable to land, timber, and buildings in the remaining towns and in the unincorporated places was considered to represent basically rural values. Dividing the total number of rural acres into the amount of tax derived as indicated gives the following rural tax per acre for representative years: \$.38 in 1913; \$1.13 in 1929; \$1.13 in 1938; \$1.25 in 1946. The figures are not equivalent to the tax on farm real estate since they inevitably include the tax on land and buildings in villages.

The situation in Michigan furnishes an interesting contrast. Farm real-estate taxes per acre here were \$.54 in 1915; \$1.38 in 1929; but only \$.44 in 1938. A special study by one of Professor Fairchild's associates (3) showed that the reasons for this decline in tax per acre during the depression years were: (a) the lowering of assessed values, (b) a constitutional amendment limiting the tax rate to a maximum of 15 mills, (c)

the adoption of the retail sales tax by the state, and (d) increased state financial aid to local governments. Local governmental costs did not decline, but other measures reduced the pressure on the property tax and virtually eliminated the demand for special forest-tax legislation in Michigan.

The state government in New Hampshire also has a narrow tax base. Its chief source of undesignated revenue is the taxation of minor "vices." A canny form of Puritanism has led to the taxation of racing, tobacco, and beer, and a mark-up on liquor sold at state stores. The purpose is to secure a maximum income which depends upon preservation of the goose that lays these golden eggs. Certain state functions such as highway construction and fish and game propagation are financed through earmarked revenues. A major reason why the state aid to local government is so skimpy is that the undesignated revenues are insufficient to permit sizable grants. The proponents of various measures for broadening the revenue sources of the state have not succeeded in uniting to push through a program. Proposals for a sales tax or a net-income tax were again killed in the 1949 legislature. A new proposal for a gross-income tax was also defeated. Rural representatives have played a prominent rôle in rejecting new taxes.

The political situation is difficult to analyze. Though the rural proportion of the total population declined from 83 per cent in 1850 to 42 per cent in 1940, the rural areas have maintained a strong position in the state legislature, with its house of 400 representatives. So tightly have the towns clung to their prerogatives that they have come to be known as the "little republics." At present it is stipulated that every town, regardless of size, shall be represented in the legislature in at least one session out of five. At the last constitutional convention a referendum providing for representation of every town at every session was drafted for submission to the voters. It almost secured the necessary support at the general election to become a constitutional amendment.

Most of the representatives of the small towns and the rural areas are Republican, but the industrial centers elect many Democratic representatives. The opposition to and the support for forest-tax reform, however, have been essentially nonpartisan. A sustained drive for a change in forest taxation dates back more than forty years. Pressure for the change has been maintained because of failure of the state to secure any adequate alternative source of revenue to lighten the property-tax load.

Spearheaded by the Society for Protection of New Hampshire Forests, the drive for forest-tax reform has had the official support of almost every organization in the state. In 1942 the state constitution was amended to encourage special tax treatment of growing wood and timber. The following year the legislature took the first step in this direction by requiring the separate assessment of growing wood and timber, though this class of property was still to be taxed at the same rate and on the same basis as other property.

Finally, in 1949 the alert regime of Republican Governor Sherman Adams gave the impetus to secure passage of the yield-tax measure. In supporting the new law the Governor brought to bear his first-hand understanding of the forest-tax problem gained as the woods boss of one of the larger pulp and paper companies operating in the state. It appears strange that the strongest opposition came from the small towns, which form the backbone of the state's Republican organization. Yet there was more logic in the rural desire to prevent reduction of the property-tax base than in the rural refusal to extend taxation to predominantly urban classes of revenue.

FEATURES OF THE NEW TAX LAW

The act relating to forest conservation and taxation which became Chapter 295 of New Hampshire Laws of 1949 is an adroit combination of answers to many previous objections to the yield tax. First, it releases nearly all classes of growing wood and timber from the general property tax and substitutes a yield tax of 10 per cent of stumpage value, to be assessed at the time of cutting. Second, the property tax on forest land is retained. Third, the yield tax is to be administered locally. The selectmen, who are the local assessing officials, will levy the tax, and the income from it will be expended for local purposes, for local control has a strong appeal in New Hampshire. Fourth, the law has been so designed that it will apply to cutting operations on the White Mountain National Forest. This has increased its popularity with north-country residents.

Much opposition to forest-tax reform has been based on the fear that the amount of local revenues either would become unpredictable or would be seriously reduced. The law takes care of this by providing for reimbursement by the state for each town to the full extent of any loss in tax revenue not covered by the new yield tax. The creation of a special state fund is authorized as a source of such reimbursements. The sum of \$300,000 can be set aside from the treasury or can be raised by issuing

bonds. The bonds, if issued, are to be retired through the annual earmarking of not more than \$25,000 from the Forest Improvement and Recreational Fund, which consists of revenues accumulated from the operation of state parks and forests.

A unique feature of the new law is an attempt to encourage forest conservation through the abatement of 30 per cent of the yield tax for cutting in accord with approved standards. The owner who qualifies for this abatement will have his stumpage taxed at the rate of 7 instead of 10 per cent of its value. Minimum cutting standards are being recommended to the state forester by the District Forest Advisory Boards. These standards are to become effective upon approval by the state forester with the advice and consent of the Forestry and Recreation Commission. It appears that the restrictions placed upon the operator through these standards will be rather nominal, at least initially.

ADVANTAGES AND DRAWBACKS OF THE NEW LAW

It has always seemed paradoxical to those unfamiliar with the workings of the New Hampshire property tax that such concern over its heaviness should go hand in hand with an amazingly small amount of tax delinquency. Passage of the law has brought into the open the extent to which the property tax on timber had been guided by the principle of ability to pay rather than by the full value. This situation has been revealed through the charge that the new tax favors the owner of large holdings, frequently a nonresident, at the expense of the resident with smaller holdings. Selectmen do not hesitate to admit now that they have had a searching eye for timber values on properties acquired by summer residents and by lumber and pulp companies. As a result, lifting of the old tax is proving beneficial to the nonresident owners while offering no relief to the resident whose timber values went relatively unnoticed. It is thought by some advocates of the new law that this may force the reconsidering of the whole question of property-tax administration. In any event it seems advantageous to have a clearer picture of the subjective interpretations of the property tax which often have prevailed in the past.

Some rural residents, however, claim the law is a screen for subsidy in the form of tax concessions to large operators under the guise of promoting forest conservation. This attitude was expressed by a number of resident owner-operators of small holdings after the passage of the law in the summer of 1949. Some stated that they intended to strip off their

timber before the new law went into effect in the spring of 1950. Fortunately for the condition of the woods, the market in the winter of 1949-50 was unable to absorb an excessive supply. Large operators generally are pleased with the law, and some are planning to expand and improve their holdings. The quieting of the antagonism of rural residents may well depend on the good faith of larger owner-operators in applying high standards of forestry to their own lands.

If it is true that much forest property in the state has been under-assessed, then the great need for forest-tax reform is not immediately evident. Aside from the unequal application of the property tax, however, the threat of sudden arbitrary increase in valuation serves as justification for the change. Once the new law is in effect, owners will have no pretext for stripping their timber to lighten their tax burden. On the contrary, the new law offers an incentive for harvesting only the higher-value timber and for building up the growing stock through preserving the lower-value young trees from premature liquidation.

A possible disadvantage of the yield tax is that owners of mature timber with recreational value will hold it off the market indefinitely if they are immune from taxation. This drawback is taken care of by a clause in the New Hampshire law stipulating that, upon attaining maturity, any timber stand may be declared by the assessing officials as again eligible for imposition of the property tax. The catch lies in obtaining a sound and generally acceptable basis for determining maturity.

Theoretically, the combined land and yield tax also has the drawback of penalizing the poorer sites if a uniform land tax is applied. This objection can be met in New Hampshire through adjustment of the land tax to the productivity of the site at the discretion of the assessing officials. Again the problem lies in finding an adequate basis for determining productivity.

A major advantage of the new law that received little publicity during the campaign for its passage is the spotlight that will be focused on the customary lump-sum timber purchases. The operator who contracts to buy timber becomes the owner in the eyes of the law. In the return that he is required to file with the assessing officials he must state the kinds and amount of timber cut. This divulging of trade secrets of the lump-sum buyers may cause reform of their practices or force them out of business. Operation on a scale purchase basis is considered more conducive to good forest practice.

Another disadvantage of the law that may prove its greatest practical

obstacle is its passage in advance of any alleviation of the overall tax situation. The \$300,000 authorized for the reimbursement fund is the sum estimated as necessary to meet the deficits of the individual towns during the first year of operation of the new law. The advocates of the yield tax have some grounds for hope that it will produce a larger revenue than originally anticipated. This hope is based on the substantial areas of underassessed timber that may come onto the market fairly continuously. If their expectations do not materialize, it may prove politically impossible to secure repeated appropriations of \$300,000 a year to keep the reimbursement fund solvent. The total of \$3,000,000 over a ten-year period is an item not to be lightly dismissed in a state which had to institute a rigorous austerity program at its last legislative session to balance its budget.

In summary, most of the obstacles to the law lie in the substitution of a new set of administrative problems for the old ones, which had become case-hardened by a long tradition of expediency. If the lack of expedient local by-passes for the new problems causes greater reliance on the guidance of the state's forestry agencies and of the State Tax Commission, the change may be a wholesome one. The major threat to the new law may prove to be the lack of adequate state financial strength to bridge the gap in yield-tax revenue while the forest resource is being built up to a higher level of sustained production. Here, too, the setting of the whole tax situation in a new perspective may foster reconsideration of their own best interests by small-town residents who have been the mainstay of New Hampshire democracy. It is a heartening step that, since passage of the law, Governor Adams has assigned two well-qualified men to serve as emissaries to the hinterland. Rural support for the law is increasing with an understanding of the contribution that its proper application can make to the rural economy.

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THE MONTANA CONSERVATION COUNCIL

A SIGNIFICANT EXPERIMENT IN CONSERVATION ORGANIZATION

KENNETH P. DAVIS

TO EVALUATE the significance of the Montana Conservation Council it is necessary to have some general understanding of the situation in which it developed. Here are a few key points.

Montana lives almost entirely on its natural resources; it is a producer of raw materials. A half million people thinly occupy its 94 million acres as compared to 6 million people on 36 million acres in Michigan. While the per capita wealth of the state is high, it is low in view of the demands its physical size places on furnishing the services we have come to expect in these United States in terms of roads, educational facilities, and the like.

The state includes very large wild-land areas, most of which are in public ownership, largely Federal. This is particularly true of forest lands, since nearly 80 per cent of the total forest area of 24 million acres is in the national forests. The activities and services of the Federal agencies in conservation are correspondingly large. Most of the technicians in the state are federally employed.

The volume and coverage of natural-resource services the state supplies are small compared to its large interest in these resources, especially as regards wild land. This is particularly true of wild lands. It has nothing approaching the Michigan Department of Conservation in conception, organization, scope, or financing. In forestry the state has a state forester and good supporting legislation. However, his office is seriously underfinanced, and his work is limited almost entirely to fire control and timber-sale administration on state-owned forests. There is a strong School of Forestry at Montana State University, which over the years has exerted large leadership and influence in forestry and wild-land conservation matters, although its actual facilities are largely limited to teaching. In agriculture the state coöperates with the Federal Government in supporting an excellent research and extension organization through the land-

grant college system. In wildlife there is an active and developing Fish and Game Department. Collectively, however, state conservation agencies are weak and particularly so as compared with those of the Federal Government.

Nevertheless, there is a large, deep, but somewhat inarticulate popular concern over the wise use of Montana's natural resources that is emerging through the atmosphere of exploitation which has dominated its history and outlook in the past. After all, the state is scarcely more than a generation removed from the actual frontier, where natural resources were something to conquer and tame. I am convinced that the people of the state have developed tremendously in their conservation awareness and thinking in recent years, but this thinking is more or less latent.

It was in this general situation that the Montana Conservation Council developed. Its immediate beginning was in August, 1948, when people representing seventeen different organizations and groups met at the state university in Missoula for a general conservation conference. The Council emerged from this conference. Its basic purpose was to serve as a common meeting ground, a popular front, through which all groups interested in conservation could be effective in furthering a more general understanding and application of conservation. The specific objective was to promote conservation education in Montana on the broadest possible basis. This was recognized by everyone as a prime need requiring concerted action for effective progress.

The Council was kept informal, with no written constitution and by-laws—nothing more formal than the motto adopted, "Conservation is everybody's business," which well expresses its general philosophy. Anyone may become a member by the simple act of participation. It happened that I was named president of the organization, being at that time in Montana, my native state, serving as dean of the School of Forestry at Montana State University.

At that meeting in August, 1948, the newly formed Council undertook two major projects. The first was an adult education project, specifically organization of a conservation caravan to make a field-study tour of Montana resources and their use. The general idea was that seeing is understanding; that only by getting key people representing various organizations and groups together on the ground for a trip of some duration could the many-sided nature and interrelations of natural-resource use be comprehended. The second job was to promote and strengthen conservation education in Montana schools.

The conservation caravan turned out to be a highly successful venture. Decision to hold a caravan tour in the summer of 1949 was made and a working committee organized. The inevitable meetings were held, and plans took form. A six-day trip in western Montana was planned in detail with an itinerary insuring a well-rounded picture of the use of natural resources in forestry, agriculture, wildlife, and recreation. Tour information was sent to many individuals and organizations, and as much publicity generated as possible. Then came the questions. Would people and organizations accept this new Council in an already complexly organized field as meaning business and offering something? Would they sponsor the sending of representatives and pay their way since the caravan and Council had no financial resources and the trip had to be self-supporting? The aim was that after the tour each individual would return to his own group able to give a broader picture of what conservation is and means on the ground. Yet organizations are understandably slow to finance sending their members on an untried venture and particularly one that might seem like a mere junket. The whole idea was new; there were no precedents.

But the idea had vitality and received support. The Montana Association of Soil Conservation District Supervisors supported the caravan and appointed representatives. The Western Montana Fish and Game Association, a forward-looking group, voted to send a high-school and an elementary-school teacher from Missoula on the tour. Winton Weydemeyer, Master of the state Grange and a deeply thinking conservationist, gave it active support and enlisted participation by the Grange people. The Montana Federation of Labor was keenly interested and sent three representatives. The various Federal and state conservation agencies gave active help, as did the University and the State College. And so the idea slowly became a reality.

By the take-off day of July 18, 1949, an extremely well-balanced group was ready to go. It included three ranchers representing the Grange and Soil Conservation District Supervisors, three lumber and sawmill workers representing the labor organizations, two housewives, a high-school student, a high-school principal, a high-school teacher, two elementary-school teachers, a businessman-sportsman representing a chamber of commerce, a lumber salesman representing the Anaconda Copper Mining Company, one member each from the Federal Forest Service, Soil Conservation Service, and Bureau of Land Management, the state extension forester, a professor of forestry, and a professor of

geography representing the University and the State College, respectively.

This was the diverse group of twenty-one people, many of them unacquainted, who faced each other in a chartered bus one Monday morning. Most of them probably secretly wondered how such a group would get along for a full week of travel. As the tour leader I, too, certainly wondered.

It worked out amazingly well, better than any of us imagined it could. The group quickly became welded together through the ready acquaintanceship of travel. Though all were concerned with conservation, individual interests were often limited in scope. This trip assembled the picture as a whole. It showed the basic interdependence and unity of mountains and valleys, of streams and crops, of timber and industry, of agriculture and wildlife. It demonstrated the common interest in conservation of dissimilar occupational groups, between housewives and sawmill workers, foresters and soil conservationists, college professors and ranchers, high-school teachers and sportsmen, trade unionists and businessmen.

The tour began with an outstanding day in the famous Bitterroot Valley in southwestern Montana. The varied natural resource situations and problems of the valley were presented mostly by landowners themselves, thirteen people taking part. The itinerary was arranged by A. J. Patterson, a Hamilton rancher, who did a remarkable job of both planning and execution. The day in the Bitterroot was followed by five more equally educational days in western Montana. While the scene changed greatly from day to day with the varied nature of the territory, the basic theme and pattern were the same. For many people, the state and its situation were viewed in a new light. A common remark was: "I've been through this country before but have never really seen it until now."

The success of the trip was largely due to two things. The first was the large number of people participating. In addition to the caravan members themselves, sixty-one local people took an active part in discussions and descriptions. Many more met the caravan from day to day and a number of them traveled with it for a day or two. The second was the fine group spirit and understanding that developed. Traveling together in a bus had much to do with this; it probably could have been achieved in no other way. A loud-speaker system made it possible to talk effectively en route and avoided many time-consuming and tiring stops. The caravaners were royally fed and entertained with the best of Montana hospitality.

The plan is to continue these tours as recurrent affairs, covering a different portion of the state each year. With an area of approximately 147,000 square miles there is ample space for three or four entirely separate tours. Two may be conducted simultaneously if the demand justifies. So much for the caravan as an experiment in adult and organization education in conservation.

Another closely related enterprise beginning independently, but later becoming more or less allied with the Council, was a series of radio programs on natural resources and their conservation given during the winter of 1948-49 in western Montana. There are a number of agencies and groups in and around Missoula interested in conservation in one way or another. It was proposed that they work together on a series of radio programs. A local radio station, KGVO, agreed to sponsor three fifteen-minute programs a week as a local-service feature, but could offer little assistance in script preparation. Over a thirty-week period ninety programs were put on by something more than twenty agencies and groups. It might be of interest to mention a few to give an idea of the range of interests involved: the Western Montana Fish and Game Association, Montana Federation of Garden Clubs, the Forest Service (both the research and the administrative branches), the Soil Conservation Service, the Farmers' Home Administration, the University (both forestry and biological science groups), the Farmers' Union, State Forester, State Fish and Game Department, Lumber and Sawmill Workers' Union, and the Missoula Chamber of Commerce.

The general theme, stated by the radio announcer at the beginning of each broadcast, was "Conservation of Your Natural Resources, the Lifeblood of Montana." Within this theme each agency or group was free to develop a program or programs built around its own interests and work.

It could not be said that all the programs were polished presentations. Scheduling ninety programs on a minimum of organization and strictly among amateurs was a difficult matter. Having served as chairman of the scheduling committee I know. I can well recall times when the radio station asked where was the next program, the call coming an hour or two before it was scheduled to go on the air. However, the programs were original, local in origin, and some of them very good. Collectively, they gave a good account of the use and conservation of resources, and their public reception was favorable. Of importance probably equal to the public benefit was the fostering of mutual acquaintanceships and better understanding among the various groups and agencies participating.

As earlier stated, the second major project of the Council was to strengthen conservation education in Montana schools. In furtherance of this a conference was called by the Council at Montana State University in the summer of 1949. The meeting was organized by the Conservation Education Committee of the Council under the chairmanship of Dr. Harold Tascher of the University. It was an excellent meeting well attended by representatives of most of the educational institutions and organizations of the state. The whole problem of conservation education in the schools and its recognition as a part of teacher training was thoroughly discussed. Constructive recommendations were made and presented to the State Board of Education and to all other agencies and organizations concerned. One concrete outcome was the holding of a conservation workshop as a part of the University's summer session of 1950. This marks a definite move to strengthen teacher training. Another specific outcome of the meeting is preparation of a bulletin on Montana's resources and their use for the schools.

Another project under the general auspices of the Education Committee, but resting primarily on the initiative and energy of a member of the Council for its execution, is initiation of a series of conservation "show-me" trips and talks at biweekly intervals for those in the sixth and higher grades in the Washington School at Anaconda. Mrs. Carolyn Madden of Anaconda, secretary of the Council, is leading this enterprise and reports enthusiastic response by students, teachers, and parents. It is an experiment in community-conservation education with large possibilities.

As shown by these various activities, the Conservation Council is on its way to becoming a force in Montana. It is an interesting adventure in relationships. The Council works primarily through its members, whether individuals or groups. Being composed of diverse elements, it can act as a unit only on matters of general import and agreement.

Its primary value is probably in bringing people and organizations together. I have seen many instances of this during the period I worked with the Council. One of them concerns the University and the State College, the relationship of which is analogous to that between the University of Michigan and Michigan State College, although in Montana all the institutions of higher learning are under the general administration of a chancellor. This does not, however, keep the University and the College from eyeing each other. From the start care was taken to avoid identifying the Council as the offspring of any particular institution, though it has been consistently maintained that overall leadership of the

Council should come from the educational institutions of Montana. Such matters put much premium on good faith and mutual trust. As concrete evidence of good relations, leadership of the Council was shifted in 1950 from the University to the State College. It is believed that the Council has been a force in strengthening rapport between these two institutions, and the same can be said as regards other agencies and groups brought together through the Council.

All in all, a fine start has been made in Montana, significant in development of that feeling of unity and wide understanding with which conservation must be approached. It is indeed everybody's business.

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RED PINE GROWTH TEN YEARS AFTER THINNING

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INTRODUCTION

RED PINE was once an important component of the famous pine stands of the Lower Peninsula of Michigan. Repeated fires after logging largely eliminated any young growth that might have partially replaced the virgin pine, so that today there is only a very small area of natural red pine. This species, however, has been a favorite one for planting. Of the half-million acres of forest plantations in Lower Michigan, probably 45 per cent are in red pine. These plantations are still in the early stages of development, and few have reached merchantability—even for small-sized material such as pulpwood.

Red pine is rated as an intolerant tree (1), but one that tends to stagnate in dense stands (4). Good response to thinning has been reported in Minnesota (5) and in Wisconsin (6). Published information on thinning of red pine on the sandy soils of Lower Michigan has been completely lacking. Consequently, any information on red pine growth and development in response to thinning in the northern part of the Lower Peninsula should be of interest.

STAND DESCRIPTIONS

Two red pine stands were selected for study by the Michigan Conservation Department in 1934. One was a densely stocked plantation representative of the earlier reforestation efforts, and the other an overstocked natural stand.

The red pine plantation is located on the Higgins Lake State Forest in Crawford County. It was established in the fall of 1912 with 3-0

stock. Trees were planted in horse-plowed furrows with a spacing of 5×5 feet. This spacing resulted in a stand of 1,740 trees per acre. The planting area was an open field that had once been cultivated for crops. The survival of trees to 1934 was 85 per cent. The site, a level area of Grayling sand, is classed as poor to medium in productivity (site index 46 at 50 years), according to site-index curves for red pine (2).

The natural stand of red pine, located on the Houghton Lake State Forest in Roscommon County, is dense and even-aged, with some scattered white pine, jack pine, and oak. From increment borings the stand was estimated to be 38 years of age in 1934. Basal scars indicate that surface fires have passed through the stand, but it is likely that this particular area escaped being heavily burned after logging. A few scattered red pines from the original stand are still present. Specific factors contributing to the establishment of this exceedingly dense stand are not known. The soil is Rubicon sand on a level and low situation. This site is also classed as poor to medium for red pine (site index 46 at 50 years).

The sites for both the plantation and the natural stand appear to be quite similar. The plantation is on a soil series (Grayling) that might be classed as poorer in productivity than Rubicon, but soil type alone is not the whole answer in evaluating sites. The cultivation of the plantation area previous to establishment improved the site at least temporarily, whereas the heavy stocking may have reduced the apparent site index of the natural stand.

THE THINNINGS

In 1934 both stands were thinned very lightly. These thinnings were so light that in 1939, five years later, the effects were hardly noticeable. About all that was accomplished was the removal of suppressed trees. In 1939 it was decided, therefore, to thin more heavily. The plantation at that time was 27 years old (30 years from seed) and was reduced to 620 well-spaced, good-quality trees per acre. The 43-year-old overstocked natural stand was thinned more lightly, since it was feared that snow breakage and windfall would result if the stand of spindly trees was opened up very much. Here 1,100 trees per acre were left. Stand conditions after thinning are summarized in Table I.

To follow the growth and development of the thinned and unthinned portions of these two red pine stands half-acre permanent plots were laid out in the thinned stands and $\frac{1}{4}$ -acre plots in the unthinned stands. Individual tree measurements consisted of d.b.h. to the nearest one-tenth inch,

total height, crown length, crown width, and crown class. In 1949, ten years later, the trees were remeasured for growth, changes in stand structure, and mortality.

TABLE I

STOCKING PER ACRE OF THINNED AND UNTHINNED STANDS IN 1939

Item	Plantation		Natural stand	
	Thinned	Unthinned	Thinned	Unthinned
Trees, number.	620.0	1,524.0	1,100.0	3,668.0
Basal area, square feet	65.0	131.3	102.2	167.9
Volume, cubic feet . . .	690.4	1,274.4	1,492.3	2,150.8

RESULTS

Diameter Growth

Diameter growth was increased considerably by thinning in both stands. The dominant and codominant trees on the thinned plots grew almost twice as much in diameter as corresponding trees on the unthinned portion of each stand (Table II).

TABLE II

DIAMETER GROWTH IN INCHES OF THINNED AND UNTHINNED
RED PINE BY CROWN CLASSES, 1939-49

Crown class	Plantation		Natural stand	
	Thinned	Unthinned	Thinned	Unthinned
Dominant.	2.52	1.28	1.86	1.32
Codominant.	2.02	.78	1.23	0.68
Intermediate	1.65	.38	.57	.21
Overtopped.24	.04

Crown dominance alone in a stand does not necessarily insure good growth, because dominance is a relative term for a particular stand. This is revealed in Table II, which shows that growth of dominant trees in different stands ranged from 1.28 to 2.52 inches at d.b.h. The best growth

was attained in the thinned plantation, where the dominant trees had very little side competition and had green crowns covering almost 60 per cent of their total height. Since the natural stand was not so heavily thinned as the plantation, growth was somewhat less. If thinned more heavily, the trees in the natural stand probably would have grown as well as those in the plantation. On the basis of results of these thinnings, it appears that an average diameter growth of two inches in ten years on crop trees can reasonably be expected in similar stands when under management.

Height Growth

Height growth was found to be closely correlated with crown class, being best on the dominants and the codominants (Table III). Of more importance, however, was the significant response in height growth made in the thinned natural stand. In contrast, height growth in the thinned part of the plantation was not significantly better than that on the check plot. Apparently the competition in the unthinned part of the plantation had not yet become severe enough to reduce height growth, whereas the severe competition in the unthinned natural stand has definitely retarded height growth.

TABLE III
HEIGHT GROWTH, IN FEET, OF THINNED AND UNTHINNED
RED PINE BY CROWN CLASSES, 1939-49

Crown class	Plantation		Natural stand	
	Thinned	Unthinned	Thinned	Unthinned
Dominant and codominant.....	11.6	10.9	11.0	8.9
Intermediate.....	...	9.9	8.7	5.4

The results indicate that it is not necessary and, in fact, not desirable to maintain a dense stand for the best height growth. On the other hand, height growth might be retarded if the stocking is reduced too severely. However, the point at which this occurs is not known.

Volume and Basal-Area Growth

Before 1939, when the plantation was twenty-seven years old, there was very little mortality due to stand competition. Thereafter the rate

of diameter growth on the untreated plot decreased and mortality increased. Thus, for its effect on growth, the thinning was made at the proper stage in the development of this plantation, which was originally planted 5×5 feet. In spite of the reduction in basal area by one half and in the number of trees by over one half by thinning, the total volume growth continued to be as good as that on the unthinned plot, and the basal area growth was higher (Table IV). The average diameter of the main stand was about four inches in 1939, so that the high cordwood growth was due primarily to ingrowth of trees to merchantable size of five inches. The thinned plot now has as much cordwood volume as the unthinned plot, and it is on much larger trees, an important feature from the economic viewpoint.

The natural stand was already fully stocked in 1934, and mortality has been severe since then. In 1939 the stand, at age 43, had almost stagnated. The thinning removed over two thirds of the number of trees and over one third of the basal area, but after the thinning there was still some mortality. Basal-area growth after thinning was almost double that on the unthinned plot, but volume growth was about the same (Table IV).

TABLE IV
BASAL AREA AND VOLUME GROWTH PER ACRE, 1939-49

Item	Plantation		Natural stand	
	Thinned	Unthinned	Thinned	Unthinned
Basal area, square feet	77.5	59.5	47.7	25.2
Volume, cubic feet....	1,381.0	1,332.0	1,159.3	1,391.2
Volume, cords *.....	18.90	15.36	13.04	13.35

* Rough cords to 4-inch top d.i.b.

From a comparison of all plots in Table IV it appears that similar young red pine stands on low to medium sites of this type are capable of producing about 130 cubic feet of wood per acre per year.

Stem Taper

Stem taper varied with stand density. The trees on the thinned plots in both stands had greater taper in 1949 than those on the unthinned plots. The trees in the natural stand had much less stem taper than those

in the plantation (Table V). This reduced taper evidently resulted from the continuous dense stocking in the natural stand.

TABLE V
RELATION OF D.B.H. IN INCHES TO TOTAL HEIGHT IN 1949

Total height in feet	Plantation		Natural stand	
	Thinned	Unthinned	Thinned	Unthinned
30	4.5	3.5	3.1	2.5
35	5.8	5.0	3.8	3.1
40	8.0	7.6	4.7	3.9

Additional evidence of the effect of thinning on stem taper can be found by analyzing diameter and height growth for the period. In both stands diameter growth per foot of height growth was highest in the thinned stands. In other words, the trees in the thinned stands were becoming stockier than those in the untreated stands. Likewise, when dominant trees are compared with intermediate trees within any stand, the dominants are found to have grown more in diameter per foot of height growth. Dominant trees were becoming stockier than intermediates.

Spacing

Spacing between trees ranged from 3.5 feet in the unthinned natural stand to 8.4 feet in the thinned plantation. Stand density given in terms of spacing alone cannot be compared between the two stands because of the differences in age and tree sizes. Spacing given as a percentage of total height of the trees (7) accounts, however, for both site and age, so that all the plots may be compared in this respect. Table VI gives a comparison of the spacing-height ratio on the different plots. The natural unthinned stand has been in a state of equilibrium in terms of the spacing figure. This figure may actually increase as the stand becomes older and thins itself. All the stands had almost the same cubic-volume growth, but the stands with higher spacing values had better diameter growth, height growth, and basal-area growth. The best overall growth was in the

thinned plantation, where the spacing value ranged from 29 per cent after thinning in 1939 to 21 per cent in 1949. The results agree with the recommendations of Eyre and Zehngraff (3) for desirable spacing-height ratio.

TABLE VI
SPACING AS A PERCENTAGE OF TOTAL TREE HEIGHT

Year	Plantation		Natural stand	
	Thinned	Unthinned	Thinned	Unthinned
1939	29	20	19	9
1949	21	15	15	9

Changes in Stand Structure

Differences in the distribution of trees by diameter classes are already evident in the plantation ten years after thinning (Table VII). In the natural stand the only evident change due to thinning is the reduction in the number of trees in the smaller diameter classes (Table VII).

TABLE VII
NUMBER OF TREES BY DIAMETER CLASSES IN 1949

D.B.H. in inches	Plantation		Natural stand	
	Thinned	Unthinned	Thinned	Unthinned
0-4	48	632	628	1,840
5-6	304	736	238	348
7-8	250	92	122	112
9-10	18	0	34	40
Over 10	0	0	26	8
Total	620	1,460	1,048	2,348

Thinning changed the distribution of trees by crown classes considerably in the plantation but to a lesser extent in the natural stand (Table VIII).

TABLE VIII

PERCENTAGE DISTRIBUTION OF TREES BY CROWN CLASSES IN 1949

Crown class	Plantation		Natural stand	
	Thinned	Unthinned	Thinned	Unthinned
Dominant and codominant.. . . .	88	68	29	28
Intermediate... . .	11	22	27	22
Suppressed...	1	10	44	50

SUMMARY

Ten-year growth measurements on plots established in northern Michigan in 1939 in a 27-year-old red pine plantation and a 43-year-old dense natural stand were taken in 1949. The following comparisons and deductions can be made from an analysis of the data:

1. Diameter growth in both stands was definitely improved by thinning. In the plantation, growth of dominant trees was nearly doubled in the thinned area. In the more lightly thinned natural stand, growth of dominant trees was increased by about 40 per cent. It appears that diameter growth of two inches in ten years on crop trees is reasonable for these stands when under management.

2. Height growth improved as a result of the thinning. In the plantation, however, the difference between height growth in the thinned and the unthinned portions of the stand was too small to be significant. In the natural stand, height growth in the thinned portion was significantly greater than that in the dense unthinned area.

3. Total volume growth per acre was about the same on all plots, both thinned and unthinned, being about 130 cubic feet per acre per year. In the thinned stands, however, this volume is being put on fewer and larger trees, which will be merchantable sooner than those in the unthinned stands. In the unthinned stand much of the growth will be lost in mortality before the trees reach merchantable size.

4. Spacing when given as a percentage of tree height appears to provide a good indication of the degree of stocking in a stand. From the data it seems that a red pine stand needs thinning when spacing of the trees is less than 20 per cent of total height.

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PART I: BOTANY AND FORESTRY

PART II: ZOOLOGY

PART III GEOGRAPHY AND GEOLOGY

PART IV: GENERAL SECTION

**ANTHROPOLOGY, ECONOMICS, FINE ARTS,
FOLKLORE, HISTORY AND POLITICAL SCIENCE,
LANGUAGE AND LITERATURE, PHILOSOPHY,**

PSYCHOLOGY

PAPERS OF THE
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ARTS AND LETTERS

EDITORS

EUGENE S. MCCARTNEY

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VOLUME XXXVII (1951)

PART I: BOTANY AND FORESTRY

"Pusilla res mundus est nisi in illo
quod quaerat omnis mundus habeat."

—SENECA, *Naturales Quaestiones*

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BOTANY

SOME OBSERVATIONS ON THE ANATOMY OF THE COMMON GERANIUM

CHESTER A. ARNOLD

ALTHOUGH the common geranium, *Pelargonium zonale* (L.) Ait., is widely used in elementary botanical teaching, the available information on the anatomy of this plant is scant. The structure of the leaves and roots, especially in relation to their physiological activities, has received some attention, but a search through the literature on plant anatomy reveals only casual references to the stem. Even these are not numerous. MacDuffie (3) and Thompson (5) give some information on the form and structure of the vessels, and Heimsch (2) refers to several anatomical features of the secondary xylem that possess taxonomic significance. Hegedüs (1) mentions the fact that independent bundles become connected by interfascicular cambium in the young stem. Metcalfe and Chalk (4) summarize the literature relating to the Geraniaceae that has appeared since the publication of Solereder's *Systematic Anatomy of Dicotyledons* in 1908.

The observations recorded in this paper were made from a set of fifty slides prepared by Triarch Botanical Products. All the sections were taken from the basal part of a potted plant about a foot high, and each slide bears a transverse and a radial-longitudinal section. Although the exact age of the plant is not known, the degree of development of the tissues indicates that in all probability it was at least a year old. The stain used was Conant's quadruple stain. Because the sections were prepared with classroom use in mind, they were cut thicker than they would have been for research purposes. If one were to undertake a thorough analysis of the geranium axis, the sections not only should be thinner, but should also be taken at several places between the apex and the base, and special stains should be applied to bring out particular features. However, regardless of the fact that the sections at hand were not prepared primarily for research, they show quite adequately details of the xylem structure, especially if supplemented with mounts of macerated tissue.

GROSS ANATOMY

The primary vascular system of *Pelargonium zonale* is a dictyostele, but an interfascicular cambium forms close to the growing point, and sections cut only a few millimeters below the apex show a complete cylinder. In all sections showing secondary growth the positions of the vascular bundles are indicated by blunt wedges of primary xylem that project slightly into the pith. Hegedüs says that the complete set of bundles is not formed by the procambium, but that some are produced by the interfascicular cambium. Between the primary xylem masses the secondary xylem comes in contact with the pith. The relation between primary and secondary tissues is shown in Plate I, Figure 1.

In the sections examined the secondary xylem is a compact layer of tissue about three quarters of a millimeter wide. The absence of well-developed rays is a conspicuous feature. The secondary phloem, which consists entirely of thin-walled cells, is one third to one half as broad as the xylem. This is succeeded by the so-called "pericycle" of the textbooks, a band of thick-walled fibers two or three cells wide. This band is interrupted at several places and parenchyma fills the breaks. A study of the origin of this layer would probably show that it is primary phloem, as has been found to be the case in *Linum* and a few other plants. The designation "pericycle" is therefore appropriate for this tissue only if it is used to distinguish it from the remainder of the phloem. There is no visible endodermis. The cortex is fairly uniform and is made up of rounded or oval cells with numerous intercellular spaces. It is about as thick as the xylem. At the stage studied there is a periderm layer, slightly thinner than the cortex, completely enveloping the stem. It is still covered with the stretched epidermis. At several places around the periphery of the section the periderm layer has split owing to increase in the diameter of the stem (Pl. I, Fig. 1 at left). Although these breaks probably perform the same function as lenticels, they lack the structure of lenticels.

DETAILED ANATOMY

Pith.—The pith, which occupies fully half of the diameter of the stem at the place where the study was made, is a relatively uniform tissue of thin-walled cells.

In cross section the pith cells are rounded and slightly faceted

because of mutual contact. Adjoining each cell are four to six triangular intercellular spaces. In longitudinal section the cells appear more nearly square and are arranged in fairly well organized vertical files. Their thin walls bear rather numerous simple pits that vary somewhat in size and shape. The only variation in cell structure within the pith is the occurrence here and there of groups of very small cells containing crystals of calcium carbonate between the ordinary cells of a file. The size of these cells and the position of the groups indicate that they originate by division of a single ordinary cell. The pith cells continue without marked diminution in size right up to the wood, although those in the outermost layer may be narrower and longer than the others. There is no medullary sheath.

Primary xylem.—The broadly triangular primary xylem masses are composed of irregularly arranged cells that contrast rather sharply with the orderly arrangement of the cells of the secondary wood. The one or two annular tracheids that make up the protoxylem are slightly immersed in the small-celled parenchyma that constitutes the point of the wedge. The innermost metaxylem consists of a few small tracheids with loosely wound spiral wall thickenings. These are larger than the protoxylem elements but smaller than those metaxylem cells that follow. The bulk of the metaxylem is composed of vessels and tracheids that are about as wide as the vessels in the secondary wood. These contain both annular and spiral thickenings, both types frequently being present in the same element. The rings are so close together that they simulate the scalariform condition, and in microtome sections it is difficult to ascertain with certainty which kind of sculpturing is present. The situation is plainly revealed, however, in macerated tissue.

Usually these spiral and annular-spiral elements extend all the way to the secondary wood, thus making up the bulk of the metaxylem. Sometimes scalariform and reticulate types intervene, but they are never abundant. The scalariform type is rare, apparently existing only where the elements are too narrow to accommodate the other form of thickening.

Secondary xylem.—The secondary xylem of *Pelargonium zonale* is a compact tissue of fibers, vessels, and parenchyma. Rays of the kind present in most secondary wood are absent. Occasionally, however, radially aligned rows of parenchyma cells extending from the

pith to the cambium constitute obscure rays, but they are never numerous. The vertical extent of these structures has not been determined. According to Heimsch (2), rays in the Geraniaceae are characteristically obscure. Wood fibers of a special kind, for which the designation "nucleate fibers" is proposed, make up the bulk of the secondary xylem (Fig. 1 *a-h*). The necessity of coining a special term for them is explained in the concluding part of this paper.

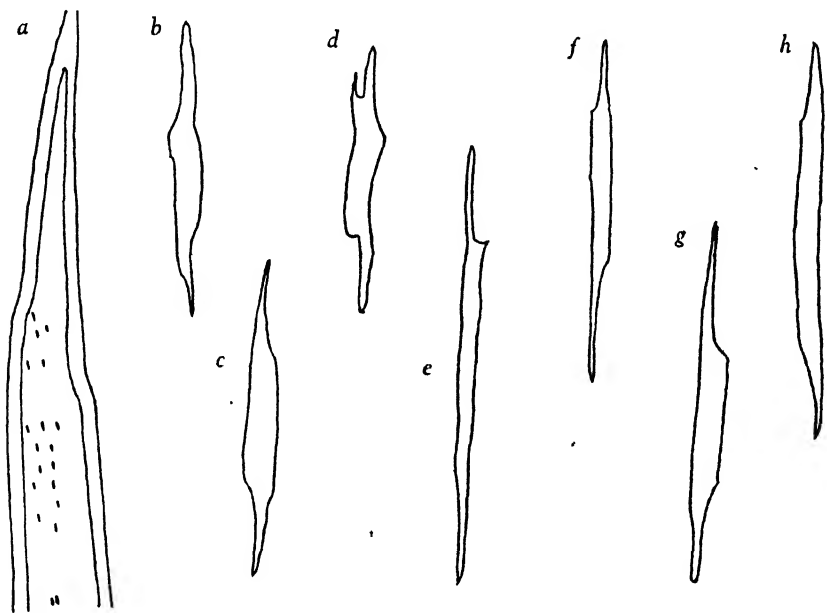


FIG. 1. *a*, terminal portion of nucleate fiber, greatly enlarged, to show distribution of the minute pits, $\times 450$; *b-h*, camera lucida sketches from mounts of macerated xylem, to show variations in size and shape of nucleate fibers. $\times 80$

The nucleate fibers are fiber-like cells with moderately thickened lignified walls and protoplasmic contents (Pl. II, Figs. 1-4), and small but conspicuous spindle-shaped nuclei. These nuclei measure about 3 by 23 microns (Pl. II, Figs. 2, 4). The walls contain very small vertically elongated pits that are about 2 microns wide (Fig. 1*a*). They appear to be simple. They are scattered over the walls, and the number on a single radial facet commonly ranges from 12 to 20, although the variation is great. They may be clustered into irregular groups of two to five or more, or they may form a multiple band along the median portion of the facet.

In appearance a nucleate fiber resembles an ordinary short wood fiber. Its oblong body portion is about as long as the cambial initial from which it was derived, but the tips became attenuated during development, so that the overall length is considerably greater. The majority of the nucleate fibers range between 240 and 750 microns in length, with approximately 50 per cent between 300 and 500 microns. The radial dimensions range between 28 and 38 microns at the widest place, and the tangential diameters are slightly less. In a specimen of average length the tapering end portions make up about half of the total length of the cell. Occasionally the tips are forked (Fig. 1*d*). Starch is frequently present, especially in those nucleate fibers near the pith.

The vessels, as seen in transverse section, are grouped into rather well organized radial rows, forming the so-called "pore chains" of wood technology (Pl. I, Figs. 1, 3). Because of the thin xylem layer in the material examined, some of the chains extend most of the way across it. Most of them, however, are short, consisting of two to four elements. Solitary vessels also occur.

In all sections, but particularly in the transverse one, the vessels stand out conspicuously because of the marked difference in size between them and the other cells. The area of the cross section of a single vessel is roughly four times that of a nucleate fiber or xylem-parenchyma cell, but, as in these cells, the radial dimension is slightly greater than the tangential one. All the walls have about the same thickness.

A vessel element is about as long as the broad part of a nucleate fiber, but bears no resemblance to it. It is an empty, nonprotoplasmic unit with walls bearing numerous large transversely oval bordered pits (Pl. II, Fig. 1). Frequently the pits are so large and numerous that there is space on the walls for only a reticulate network of secondary wall substance. Occasionally, however, they are small and fewer.

In a normal vessel element the single nearly round perforation is situated in the slightly oblique end. It is surrounded by a rather wide perforation rim, which reduces the area of the opening to two thirds or less of the area of the end. Small pits sometimes occur in the rim around the opening (Pl. I, Fig. 2). A lateral opening, in addition to the two end openings (Pl. II, Fig. 1) and long slanting ends with the perforations some distance from the extremities, have

been observed. Such variations from the typical form are infrequent but not exactly rare.

In transverse section the xylem-parenchyma cells are not easy to distinguish from the nucleate fibers because both have similar diameters, protoplasmic contents, and thickened walls. But their large pits are conspicuous in the end walls whenever these show in the section.

In longitudinal section some of the xylem-parenchyma cells are square and some are oblong (Pl. II, Fig. 3), and they are arranged in strands that are about as long as the vessel elements. The terminal cells of these strands have tapering or slanting ends. The pits in the transverse walls appear to be simple.

These parenchyma cells, which are distinctive among cells of this kind because of their thick walls and characteristic pitting, seem to ensheath the vessel elements almost completely, and, where vessel groups are close together, they constitute most of the tissue between them. The extent of continuity of the xylem-parenchyma tissue is difficult to determine because of the similarity of the cells in cross section to the nucleate fibers. Almost the only distinctive features of the parenchyma cells are the prominent pits in the cross walls and the slightly denser protoplasmic contents.

Xylem parenchyma is most abundant in the inner part of the secondary wood, especially opposite the primary xylem areas. Those cells near the primary xylem have noticeably thinner walls than the others.

The storied arrangement of the secondary xylem elements is a conspicuous feature in the radial section (Pl. II, Fig. 4). It can usually be seen extending from the inner limits of this tissue across the cambium and through the secondary phloem. It begins abruptly at the outer limit of the metaxylem.

DISCUSSION

The term "nucleate fiber" is proposed for the pointed secondary xylem elements in *Pelargonium zonale* in view of the apparent lack of any other suitable name for them. I have referred to such fibers as "substitute fibers," and among anatomical terms in current use this one is probably the most suitable. However, the Committee on Nomenclature of the International Association of Wood Anatomists has recommended that its use be discontinued because the cells that

it has always referred to are parenchyma cells. The committee has proposed the term "fusiform wood parenchyma" instead. In this particular instance, however, "fusiform wood parenchyma" is not an appropriate term to replace "substitute fiber" because it would be applied to cells that are essentially fibers and also because there are other cells present that do belong to the parenchyma category. Regardless of their shape, cells that the committee would designate as fusiform wood parenchyma do not belong to the fiber category. They are merely wood parenchyma chain initials that remain single cells.

The desirability of reinstating the term "substitute fiber" for the cells under consideration has been examined, but if it were adopted, it would then be used for something different from that for which it it was originally proposed. Another objection to its use in this instance is that the nucleate fiber is not a cell that has replaced something, as the name "substitute fiber" would connote, but from the standpoint of both origin and structure is a genuine fiber. Its peculiarity is that it contains a protoplast. In most plants the protoplasts disappear as the final step in fiber development, and the cells become essentially nonliving entities. In *Pelargonium zonale* the process stops before the protoplast disintegrates.

Although thick-walled living cells are common in plants, their occurrence has never been comprehensively studied. This neglect is sharply reflected when one is confronted with such problems as the proper designation of the living fiber cells of *Pelargonium zonale*. Fibers, whether in the xylem or elsewhere, are almost always assumed to be empty, or, at least, to be nonprotoplasmic units. As a result, any thick-walled pointed cell is called a fiber, and by virtue of this assertion the cell is regarded as being nonliving. It may become necessary to reclassify some of these cells in the light of newer knowledge.

Some of the evolutionary trends in *Pelargonium zonale* are revealed in the anatomy of the stem. Although potted specimens look like herbs, the plants become shrubby when they are grown out of doors. Even potted specimens are atypical herbs in some respects. At least they depart from conventional textbook characterizations of herbs. These departures include retention of certain woody-plant traits, among which are the perennial habit and the meristems that continue to be active year after year. Then the

periderm, which may accumulate for several years without exfoliation, is obviously a holdover of a tissue which in the ancestor of the modern species produced detachable phellem.

The ancestor of *Pelargonium zonale* was probably a woody perennial of arborescent habit. Its secondary xylem in all likelihood consisted of wood fibers or fiber tracheids, parenchyma, vessels, and probably rays, although the fact that obscure rays occur throughout the family shows that the ordinary ray disappeared early in the evolutionary history of the family before the separate genera had become segregated. The only evidence in *P. zonale* that its ancestors ever possessed rays is the occasional presence of radially directed rows of xylem parenchyma cells.

It may also be assumed that the ancestor of *Pelargonium zonale* was a plant in which maturity of the wood fibers was attained when wall thickening was complete and the protoplasts had disintegrated. Mature fibers probably formed at only a very short distance inward from the cambium, as in most modern woody and shrubby plants. But during the ontogeny of the elongated xylem elements the protoplast persisted longer and longer in those cambial derivatives that served as fiber initials. Finally, the protoplasts failed to disappear, and the fibers were carried over into the mature wood as living cells.

The retention of living fibers in the mature wood of *Pelargonium zonale* cannot be interpreted as reversion to a primitive condition, but is a new development. Just what kind of cell first gave rise to the tracheary elements during the initial stages in the evolution of the vascular system, we do not know, but primitive plants in general are characterized by a high degree of uniformity in the kinds of tracheary elements which are consistently tracheids. The fiber tracheids, fibers, and vessels of higher plants are supposed to be modifications of the primitive and generalized tracheid. But not even in the lowest vascular plants (Psilophytales, Lycopodiales, and primitive Filicales) do the tracheids of the mature stem contain protoplasts. If, therefore, the condition revealed in *Pelargonium* were a reversion to the ancestral state, this plant would be expected to show intermediate stages between fibers and tracheids, or between vessels and tracheids. This, however, is not so. Instead, the types are sharply differentiated. In fact, the fibers and vessel elements are more unlike each other in *Pelargonium* than in most other plants. The remote ancestral condition, the condition that antedated the angiosperm level,

is probably revealed in the primary xylem, where we find both tracheids and vessels that are alike in size and wall sculpturing, and it is significant to note that the primary tracheids are nonprotoplasmic. The thick-walled, minutely pitted, pointed nucleate fiber of *Pelargonium zonale* is a highly evolved cell that has been derived from a wood fiber of the usual type. The vessels, on the other hand, have evolved along more usual lines. They show some distinctive features, but are essentially like those in other plants.

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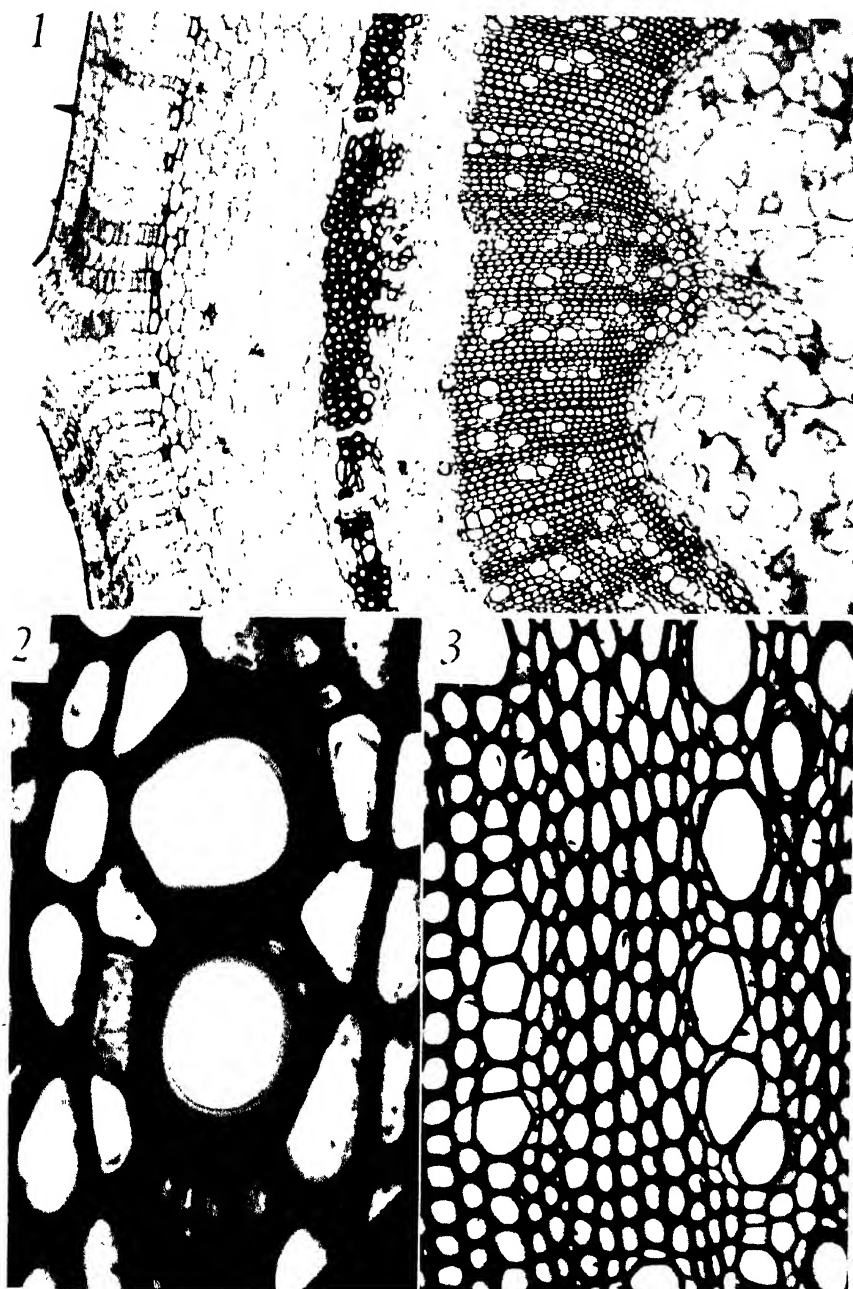
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EXPLANATION OF PLATE I

FIG. 1. Transverse section of portion of stem. $\times 30$

FIG. 2. Small portion of transverse section, showing the perforation rims of two vessel elements and adjoining parenchyma cells. The perforation rim of one element contains bordered pits. $\times 780$

FIG. 3. Transverse section, showing "pore chains," intervening parenchyma, nucleate fibers, and absence of rays. $\times 110$



Pelargonium zonale

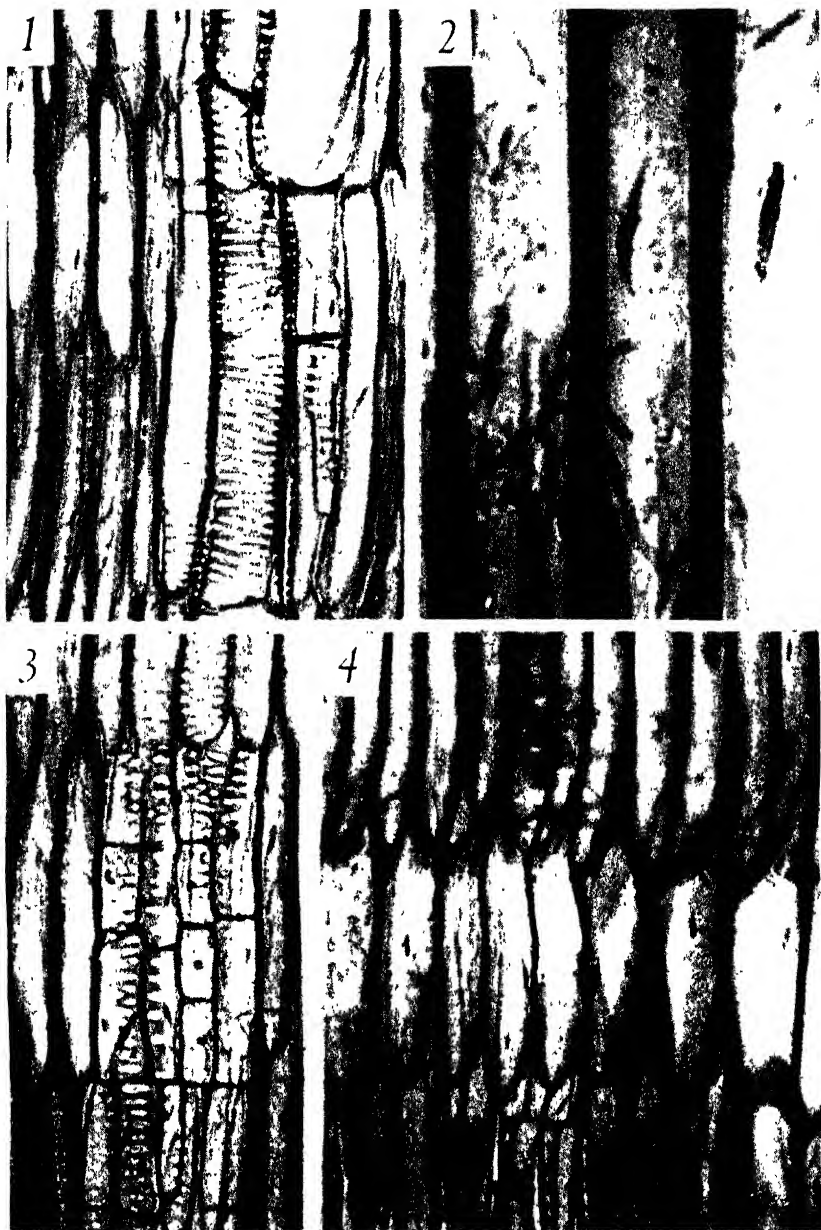
EXPLANATION OF PLATE II

FIG. 1. Radial section, showing nucleate fibers (at left) and vessel elements with characteristic pitting. One vessel element contains a lateral perforation $\times 130$

FIG. 2. Enlargement of portion of three nucleate fibers, showing nuclei. $\times 800$

FIG. 3. Radial section, showing a layer of wood parenchyma cells in the immediate vicinity of vessels not included in section $\times 130$

FIG. 4. Radial section, showing storied arrangement of nucleate fibers. $\times 130$



Petargonium zonale

BOTANICAL AND ETHNOBOTANICAL STUDIES IN THE ALEUTIAN ISLANDS

I. ALEUTIAN VEGETATION AND ALEUT CULTURE*

THEODORE P. BANK, II

ANY study of primitive man should include an evaluation, as thorough as means permit, of his environment, including the various ecological factors brought into play by the terrain, climate, plants, and animals. During eighteen months of 1948-49 and during the summer of 1950 the writer had an opportunity to make phytoecological observations among the Aleutian Islands while undertaking for the University of Michigan a series of botanical and anthropological studies. Plant collections were made on seventeen of the islands, ranging from the Alaska Peninsula to Attu, the westernmost island. In another paper the writer has presented results of a series of phytoecological studies on old village sites in the Aleutians, made with the object of defining the vegetational differences resulting from human occupancy and of using these differences, if possible, as an aid to archaeology.¹ Since it contains a thorough description of the configuration, size, and vegetation of Aleutian village sites, there is hardly any reason to repeat any of the data. It is pertinent to note, however, that the sites were all coastal in situation, and presented the archaeological remains of primitive semisubterranean, sod-covered

* Contribution from the Department of Botany and the Botanical Gardens of the University of Michigan. I wish to acknowledge my sincere appreciation to H. H. Bartlett for his untiring efforts, as director of the Botanical Gardens, in support of the Aleutian Project during the four years that it has been active and for his help and advice in preparing this paper. Appreciation is also expressed to L. H. Jordal, a member of the 1949 expedition, who helped to identify the higher plants, and to A. Harvill, who identified the bryophytes. The research could not have been accomplished without the initial support of the Office of Naval Research and, later, that of the Michigan Memorial Phoenix Project, both of which contributed research funds. To the officers and men of the U. S. Navy, Army, Air Force, and Coast Guard and the personnel of the Alaska Native Service, all of whom furnished invaluable assistance in our field work, I am greatly indebted.

¹ This article will be published in elsewhere.

houses with whale-rib and driftwood supports. The Aleutians, prior to the coming of the white man, had populous villages located upon most of the more than sixty islands.

TOPOGRAPHY AND CLIMATE

The Aleutian Arc consists of about twelve large islands and fifty smaller ones, with more than a hundred offshore pinnacle rocks and islets upon which vegetation occurs. Descriptions of their rugged configuration, many active volcanos (Pl. II, Fig. 1; Pl. V, Fig. 2), treacherous reefs and rip tides, and uniformly inhospitable weather have been given by early Russian, English, and American explorers, by the anthropologists Jochelson (8, 9) and Hrdlička (5, 6), the naturalist William Dall (3, 4), and the botanist Eric Hultén (7), as well as by many casual visitors. Criticism of the islands' inhospitality has been perhaps most graphically presented by recent G.I.'s who found themselves stationed in the Aleutians. The writer will not attempt to repeat a full description of their topography and climate except to summarize certain meteorological data.² Table I presents figures for temperature, cloudiness, precipitation, and wind velocity for the period October, 1942, through September, 1948.

During the period for which data are at hand, February and March were consistently the coldest months of the year, and the lowest temperatures recorded were 11° and 12° F. In August and September, the warmest months, the highest temperature recorded was 75° F., in September. The mean daily maximum temperature during August and September was 54° F. Such uniformly temperate conditions no doubt made it possible for the Aleut to wear the clothing he did, which was, even in winter, primarily of gut, bird feathers, and woven grass.³

Scattered clouds to clear-sky conditions were most common during the winter months, but in no year was it clear during more than 1.8

² From records made available to the writer by the Officer in Charge of Meteorological Units, U. S. Navy and U. S. Air Force, Davis Air Force Base, Adak, Alaska, 1949.

³ Early descriptions by Sarychef, Tolstykh, Sauer, and Veniamenof as reported in Jochelson (9) and Hrdlička (6) state that the main clothing of the Aleut at about the date of Russian discovery was a long nightgown-like *kamleika* of seal and sea-lion gut. Some wore fur jackets of seal, sea-lion, and sea-otter skin. The women and children often wore feather jackets (especially of puffin feathers) and capes of woven beach grass. Most of the Aleut had no covering for the feet, even in winter.

TABLE I
CLIMATOLOGICAL DATA FOR ADIAK, ALEUTIAN ISLANDS, AT SEA LEVEL DURING OCTOBER, 1942, THROUGH SEPTEMBER, 1948

Temperature: Degrees Fahrenheit												
Mean	Mean maximum	Mean minimum	Highest	Lowest								
40	44	36	75	11								
Sky condition: Percentage of time												
Clear	Scattered	Broken	Overcast	Obscured								
0.9	8.3	25.5	64.7	0.6								
Average monthly precipitation: Inches												
Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
19.2	16.3	12.9	3.6	0.6	0.0	0.0	0.0	0.0	0.6	4.6	13.3	
4.72	4.46	3.48	3.38	2.20	1.38	2.38	4.36	3.77	5.35	5.95	5.89	
Wind velocity: Miles per hour												
Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
15.8	16.5	16.5	15.2	14.5	11.9	12.8	13.7	14.9	16.8	14.7	15.9	
89	100	85	72	58	60	64	58	81	69	79	84	
SW	WNW	SW	W	W	SW	SW	SW	SW	SW WNW	SSW	SW	

per cent of the time. The period of greatest overcast (78 per cent of the time) occurred during the months of June, July, and August. Our field parties recorded for the middle part of the Aleutian Chain a total of less than 60 hours of sunshine for the three months, July, August, and September during the three years 1948-50 (Bank, 1)—20 hours a year! Aleutian winds are uniformly high and variable in direction. Gusts are frequent, especially during October and November and again during January, February, and March, often reaching 120 miles per hour. Wind velocities (Table I) were taken at a station less than 50 feet above sea level, as were the other weather observations. Although the mountaintops may sometimes extend above the cloud layer and receive more sunlight, they are most of the time bathed in fog and clouds. Especially during the summer months the interior parts of the islands are somewhat wetter than the shore, except on the higher slopes where desiccating winds have a counter-acting effect. More snow accumulates in the interior valleys than at the shore. Wind velocities seem consistently higher as one leaves the sea to journey inland, and during the winter the ridges are constantly swept bare of snow. Winter walking in the alpine regions is almost impossible. Lower temperatures than any recorded at sea level prevail even a few miles inland, and winter temperatures of mountain ridges go considerably below 0° F.

The high winds, more than any other factors, have probably been responsible for restricting the Aleutian flora and have greatly modified the way of human life on the islands. Dressed only in flimsy clothing and usually barefooted, the Aleut was probably unable to journey very far above the beach during the winter months. Jochelson (8) and Hrdlička (6) give the impression that maintaining the ancestral custom of gaining their livelihood from the resources of the sea accounted for their living at the shore.

PLANT HABITATS

In an effort to describe the vegetational features of the Aleutians, the writer has studied the distribution of the major plant habitats. Although there are additional microhabitats which will repay study, those which are sufficiently extensive and typical to show by mapping have been classified. Beginning at the seashore and proceeding inland, we find a series of sites which occur with minor variation on practically every island along the Chain. A schematic profile of

two typical islands is presented in Figure 1 to illustrate the habitat relations. Beginning with the sea the habitats are:

- I. Shoreline: everywhere rugged and rocky, with a few large, protected harbors but with many smaller bays, inlets, coves, and bights (Pl. I, Fig. 1).
 - A. Reef: usually of wave-cut basalt extending from every point of land and present also in many of the bays; inhabited by abundant edible Algae and animals.
 - B. Shore wall (cliff): wave-cut, often presenting tall pinnacle rocks and offshore islets; in places rising directly from the sea; elsewhere a rampart of high cliffs behind a narrow beach; inhabited by a myriad sea-bird population.
 - C. Beach: generally of cobble and strewn with huge boulders, but frequently (usually in bays and inlets) of gray to black sand.
 - D. Grass-thicket zone:
 1. Marginal ridge: often several such ridges or old beach lines lying in succession behind the present beaches; thick with grasses.
 2. Grass hummock: highly irregular, hummocked surface thickly overgrown with grasses, many edible plants, and plants used in weaving.
 3. Intermarginal depression: behind the marginal ridge; marshy during some seasons and containing a number of the medicinal plants. If there are several parallel marginal ridges, there are corresponding parallel inter-ridge depressions.
- II. Lower grass meadow: extending from above the beach to varying altitudes but characterized by a heavy growth of grasses, ferns, and other lush vegetation, much of it used by the ancient Aleut.
 - A. Stream valley: broad and U-shaped on larger, mountainous, islands; practically nonexistent on the lower, platform, islands (Fig. 1; Pl. I, Fig. 2).
 1. Stream margin: wet and usually rocky. Streams and lakes are abundant in the Aleutians; larger streams near the sea contain many salmon and trout during the summer and early fall.
 2. Ravine bank: steep, fern-covered, and interfering with inland travel (Pl. III, Fig. 1).
 3. Drainage flat: wet area above stream but below surrounding stream valley slopes and receiving drainage from them.
 4. Knoll or plateau: usually comparatively dry and covered with a thick mat of *Empetrum*, mosses, and lichens, together with many edible berries (Pl. IV, Fig. 1).
 5. Meadow slopes: sometimes steep and usually dissected by ravines, which, with drainage flats, make walking across them difficult.
 - B. Lake depressions: especially abundant on the platform islands and occurring even at high altitudes wherever shelves or other flat extensions of the mountain are to be encountered (Pl. IV, Fig. 2).
 1. Shallow water flat: depth of water varies considerably during year.
 2. Marginal ooze: marshy transition zone between water and higher ground. (Here are many medicinal plants!)
 3. Drainage slopes: wet and usually gentle slope rising away from the lake to dry knolls, plateaus, or better-drained meadow slopes.

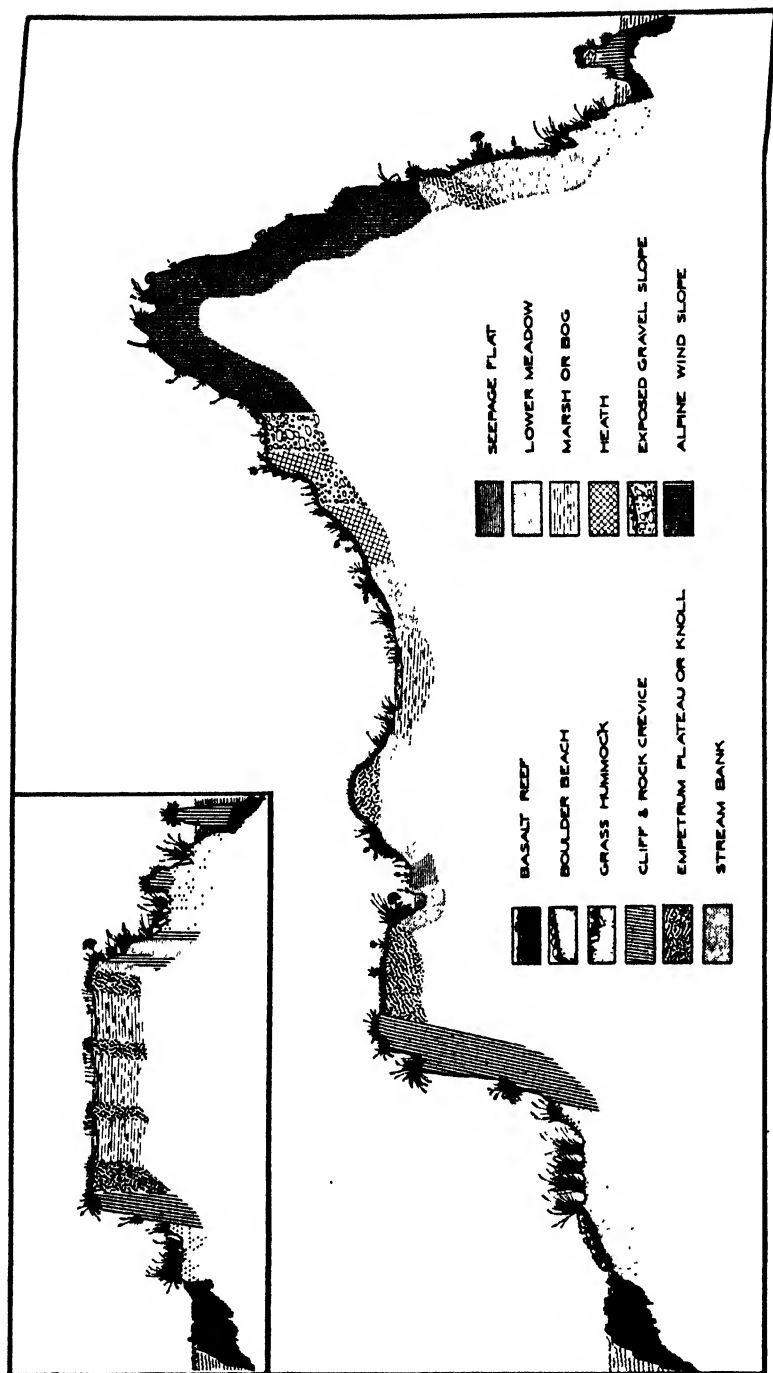


FIG. 1. Diagram representing the topographic relations of the chief habitats on the two main types of island in the Aleutian chain, namely, the plateau island (at upper left) and the mountainous island (below). The physiognomy of the vegetation is hinted at by the marginal profile. Adjacent to each part of the profile is a symbolic indication of the corresponding plant association or community, which is to be interpreted by reference to the plant lists given in the text

- C. Marsh or boggy area: usually small but sometimes extensive, especially in broader stream valleys (Pl. III, Fig. 2).
1. Mudflat: usually drying up during certain periods.
 2. Standing water marsh: unstable ground often deep enough to mire heavy vehicles; contains a number of medicinal plants.
 3. Seepage slopes: often at high altitudes in the middle of dry meadows or heath areas. These are like running sores in the mountain slopes where underground drainage comes to the surface.
- III. Rock cliff: at the upper limits of the meadows, often successive vertical walls rising from the stream valleys and ravines, and effective barriers to inland travel.
- A. Rock-face niches and crannies: crevice soil deposits and shelf extensions support a varied plant growth.
 - B. Seepage slopes: wet, alga- and moss-covered areas usually at the base of a cliff or in the bottoms of crevices.
- IV. Wind slopes: higher slopes where wind is a dominating factor in determining the vegetation.
- A. Heath zone: covers large areas of the islands where the high winds have a desiccating effect even if the relative humidity is high.
 - B. Exposed gravel areas: eroded exposed soil or gravel; found frequently on narrow terraces at upper altitudes.
 - C. Talus: usually barren.
 - D. Alpine mountaintops: extremely rocky, windy, and cold; with lichens, moss cushions, and thin *Empetrum* mat (Pl. V, Fig. 1-2).
- V. Special habitats:
- A. Bird mound: common on most ledges and hills near the sea; formed by vegetation growing in the droppings of numerous sea birds through centuries (Pl. VI, Fig. 1).
 - B. Steam jets and hot springs: fairly common on slopes of active volcanoes and along the seashore below them (Pl. VI, Fig. 2).
 - C. Salt marsh: infrequent
 - D. Village sites: along coasts of all islands, especially in bays, on points of land, and isthmuses.
 - E. Glacial margin: occurs in upper valleys of larger, mountainous islands.

Shoreline Vegetation

Sea cliffs and soil patches among beach boulders contain growths of lichens and certain mosses, for example, *Pohlia cruda* (H.) Lindb., *Plagiothecium Roseanum* (Hyp.) Bry. eur., and *Brachythecium albicans* (H.) Bry. eur.; species of *Poa*, *Potentilla villosa* Pallas ex Pursh, *P. nana* Willd. ex Schlecht., *P. palustris* (L.) Scop. (principally east of Unalaska), and *Saxifraga bracteata* D. Don.

Between the boulder zone and the grass hummocks there are usually small patches of gray to black sand or small cobbles and driftwood with at least scattered growths of *Cochlearia officinalis* L.

and *Lathyrus maritimus* (L.) Bigel., as well as a few grasses. Above this and sometimes encroaching upon it will be found the very common grass hummocks of Aleutian beach slopes. These hummocks, principally of *Elymus arenarius* L. ssp. *mollis* (Trin.) Hult., are often extremely high. They may be taller than a man's head and present a real problem to one attempting to cross them. Such an attempt usually results in frequent tumbles into the narrow deep spaces between the unstable hummocks. Associated with *Elymus* are a number of mosses and higher plants, among which the following are the most common: *Lathyrus maritimus* (L.) Bigel. (on the seaward margin), *Senecio Pseudo-Arnica* Less. (often growing three feet high), *Honckenya peploides* (L.) Ehrh., *Festuca rubra* L. (very common in the Aleutians), *Claytonia siberica* L., *Cerastium Fischerianum* Sér., *Phleum alpinum* L. var. *americanum* Fournier, *Mertensia maritima* (L.) Gray, *Stellaria calycantha* (Ledeb.) Bong., *Clayopodium Bolanderi* Best, and other mosses.

When hummock zones are lacking, their place is usually taken by dense *Elymus*-*Phleum* stands on uneven drained slopes or by areas of direct transition to a lower meadow, heath area, or cliff.

Lower Grass-Meadow Vegetation

Above the beaches, except where cliffs occur, there is usually a series of habitats which may be conveniently grouped and termed "lower grass-meadow." Each stream valley, for instance, presents a sequence of habitats from the water's edge to higher ground. In the water and attached to rocks may often be found *Fontinalis neomexicana* Sull. & Lesq., *Ranunculus aquatilis* Schlecht. var. *capillaceus* Ledeb., and *Myriophyllum spicatum* L. The writer collected these aquatic species on Umnak, Adak, and Atka islands.

Growing along the stream margin are *Streptopus amplexifolius* (L.) DC., *Linnaea borealis* L., *Juncus balticus* Willd., various grasses, ferns, *Carex* species, and, especially in the western Aleutians, *Veratrum album* L. ssp. *oxysepalum* (Turcz.) Hult. and *Veronica americana* Schwein. We also found on Attu scattered clumps of *Sorbus sambucifolia* (Cham. & Schlecht.) Roem. *Leptarrhena pyrofolia* (D. Don.) Sér. is found in the spray of waterfalls but less commonly west of Adak, and *Petasites frigidus* (L.) Fries occurs scattered next to high mountain streams. Among the stream-margin mosses are found

Hylocomium splendens (H.) Bry. eur., *Rhytidiadelphus loreus* (H.) Warnst., *R. squarrosus* (H.) Warnst., and *Antitrichia curtipendula* (H.) Brid.

Growing on the steeper banks of streams (Pl. III, Fig. 1) are *Streptopus*, various ferns, among them *Athyrium Filix-femina* (L.) Roth. and *Dryopteris oreopteris* (Ehrh.) Maxon, as well as *Claytonia siberica* L., and *Artemisia*, especially *A. unalaskensis* Rydb. var. *aleutica* Hult. Where the bank is well drained there are found *Lycopodium clavatum* L., *Anaphalis margaritacea* (L.) Benth. & Hook. var. *occidentalis* Greene, *Achillaea borealis* Bong., and *Epilobium angustifolium* L. var. *macrophyllum* (Hausskn.) Fern. as well as *E. anagallidifolium* Lam. (not too common on all islands). Also occurring here are *Galium Aparine* L., which is often a seashore plant, *Antennaria dioica* (L.) Gaertn. (scattered), and *Rhinanthus groenlandicus* Chabert. *Carex macrochaeta* C. A. Meyer is the most common sedge. Especially in the spray near falls and growing in seepage areas are *Saxifraga punctata* L. ssp. *insularis* Hult., and *Leptarrhena pyrolifolia* (D. Don.) Sér. Occurring on dryer banks are *Geranium erianthum* DC., *Aster peregrinus* Pursh (*Erigeron*), which also is frequently found at higher altitudes, and such grasses as *Festuca rubra* L., *Agrostis* species, and *Deschampsia beringensis* Hult., which are common across the Chain. *Rhododendron kamtschaticum* Pallas and *Vaccinium ovalifolium* Smith are fairly common along the steep, dryer mountain-stream valleys, the latter being more restricted to the western islands.

Almost universally there is present above the stream a flat, wet area which collects drainage from the slopes around it (Fig. 1). This flat usually itself drains into the stream and seldom has standing water, although it is almost continually wet. Commonly found here are several species of *Platanthera*, especially *P. hyperborea* (L.) Lindl., *P. dilatata* (Pursh) Lindl., and *P. tipuloides* (L. f.) Lindl., the latter occurring primarily in the western islands, but rarely elsewhere. *Orchis aristata* Fisch. ex Lindl., *Fritillaria camschatcensis* (L.) Ker-Gawl., *Polygonum viviparum* L., *Pinguicula vulgaris* L., *Aster peregrinus* Pursh, *Epilobium Behringianum* Hausskn., and other plants also inhabit these drainage flats. Occasionally *Cypripedium guttatum* Swartz is found here. Clusters of this species occurred in two widely separated localities, Adak and Unalaska, but

it has been reported from other islands. Iris, Arnica, sometimes Mimulus, *Angelica lucida* L., low grasses, liverworts, and mosses of various types frequently inhabit the flats.

In places covering large areas, especially in the broader stream valleys, but elsewhere separating the stream margin from the dry Empetrum knolls above by only a narrow strip, are to be found the fairly well drained, thickly carpeted valley meadows. These are usually gentle to moderately steep slopes, covered with tall grasses, umbellifers, and invaders from the heaths above and the wet habitats below. Erigeron, Platanthera, Fritillaria, and Epilobium invade from the stream valleys and from above have come such species as belong more properly to the alpine habitats, for example, *Lupinus nootkatis* Donn ap. Sims, *Anemone narcissiflora* L. var. *villosissima* DC., and others. Thickly covering these valley meadows are *Calamagrostis Langsdorffii* (Link) Trin., which is perhaps one of the most common grasses in the islands, along with *Deschampsia beringensis* Hult., which runs a close second. *Heracleum lanatum* Michx., *Angelica lucida* L., *Pedicularis Chamissonis* Steven., *Anaphalis margaritacea* (L.) Benth. & Hook. var. *occidentalis* Greene, *Geum calthifolium* Menzies, *Aconitum kamtschaticum* Pall. & Schlecht., *Epilobium angustifolium* L. var. *macrophyllum* (Hausskn.) Fern., *E. Behringianum* Hausskn., and *E. glandulosum* Lehm. make up a large part of this vegetation. *Epilobium latifolium* L. and *Castilleja unalaschcensis* (Cham. & Schlecht.) Malte occur abundantly, especially in the eastern islands, whereas species primarily of the western islands include *Senecio palmatus* (Pall.) Ledeb., *Sorbus sambucifolia* (Cham. & Schlecht.) Roem., *Chrysanthemum arcticum* L., and *Cirsium kamtschaticum* Ledeb. ex DC. Occurring in scattered patches is *Trientalis europaea* L. subsp. *arctica* (Fisch.) Hult., and *Ranunculus occidentalis* Nutt. subsp. *insularis* Hult. is fairly common, especially near streams. *Maianthemum dilatatum* (Howell) A. Nels. & T. Macbr. is found as part of the valley-meadow vegetation wherever drainage is poor.

Hultén has presented a profile of characteristic vegetation bordering lakes and extending from them to higher and drier ground. It is hardly necessary to repeat his listing. Many species bordering streams also occur near the lowland lakes, especially species of *Carex*, *Scirpus*, *Juncus*, and *Polygonum* (Pl. IV, Fig. 2). *Caltha palustris* L. is often found along the lake margins at least as far west as Tanaga.

Petasites frigidus (L.) Fries has also been found fairly commonly, especially at higher altitudes.

Common throughout the Aleutians are boglike areas in the sides of hills both at lower altitudes and in the alpine regions. These are seepage slopes and are essentially oozing underground drainage from the hills above. They often occur in the center of an otherwise dry heath slope. Their vegetation consists mainly of mosses and liverworts, but frequently found in them are *Mimulus guttatus* DC. (at low altitudes), *Viola Langsdorffii* Fisch. in DC., *Leptarrhena pyrofolia* (D. Don.) Sér. (not common in the west), *Pinguicula vulgaris* L., *Rumex Acetosella* L., and *Saxifraga punctata* L. subsp. *insularis* Hult. Mosses of these seepage areas include *Sphagnum capillaceum* (Weis.) Schrader., *S. Girgensohnii* Russ., *Rhytidiadelphus triquetrus* (H.) Warnst., *Girgensohnia ruthenica* (Weim.) Kindb., *Plagiothecium undulatum* (H.) Bry. eur., *P. Muellerianum* Schimp., *Pleurozium Schreberi* Mitt., *Dicranum Bonjeanum* De Not., *D. majus* Smith, *Brachythecium washingtonium* Grout, *Cirriphyllum piliferum* Grout, *Mnium punctatum* H., *Oligotrichum parallelum* (Mitt.) Kindb., and *Bryum turbinatum* (H.) Schwgr. Such zones of unstable, extremely wet and boggy ground often require long detours when one is botanizing in meadows above the beaches.

Marsh vegetation closely resembles that of the lake margins, and it is true that many Aleutian marshes are lakes which have partially dried. They are common along the shores of bays and inlets, at the mouths of larger streams, and along the bottoms of broad stream valleys (Pl. III, Fig. 2). Others occur frequently, as at Atka, on higher ground, where a flat area is surrounded by hills. Most often they are found to contain a central "puddle" or small stagnant pond. Such areas are very common west of Adak, where many of the islands are essentially plateaus rising above the sea, whose surfaces are all marshland dissected by occasional grass hummocks or moss knolls. There are no true bogs in the Aleutians of the type found extensively in Alaska, Canada, and north-central United States. Floating sphagnum mats are not to be found. The areas most closely resembling bogs are the seepage slopes already described, but they are usually not deep; they result from hillside drainage and fluctuate in size with changing weather conditions.

The vegetation of the marshes varies according to the amount of standing water present. Typically, however, one finds *Polygonum*

viviparum L., *Eriophorum medium* Anders., *Carex rariflora* (Wahlenb.) Smith subsp. *stygia* (Fr.) N. J. Anders., *Scirpus caespitosus* L., *Iris setosa* Pall. ex Link, *Geum calthifolium* Menzies, *Aster peregrinus* Pursh, *Conioselinum Gmelini* (Cham. & Schlecht.) Coult. & Rose, *Matricaria matricarioides* (Less.) Porter, *Plantago macrocarpa* (Cham. & Schlecht., *Juncus ensifolius* Wikstr. (more common toward the east), *Juncus balticus* Willd., and *Caltha palustris* L. The writer found occasional areas where *Menyanthes trifoliata* L. was common. This plant was considered by the Aleuts of Nikolski an extremely powerful medicine for stomach disorders.

Characteristic of the better-drained hilltops at lower altitudes is the sometimes thick Empetrum-moss-lichen mat (Pl. IV, Fig. 1). These mat areas are easily picked out from the air, since they show up as much darker splotches on most hilltops (Pl. I, Fig. 2). During the rains of spring and early fall the Empetrum mats are like water-soaked sponges, and water squirts from them when they are stepped upon. Although never thoroughly drying out, they are, nevertheless, dry enough at other times to provide a truly comfortable mattress for a tired hiker. Their vegetation includes *Empetrum nigrum* L., *Lycopodium clavatum* L., *L. sabinaefolium* Willd. var. *sitchense* (Rupr.) Fern., *L. annotinum* L., *L. Selago* L., and *L. alpinum* L. (the last species at higher altitudes). Lichens, especially *Cladonia*, form much of the mats, as do mosses, including the following: *Brachythecium albicans* (H.) Bry. eur., *Racomitrium lanuginosum* (H.) Brid., *Pogonatum alpinum* (H.) Brid., and others. *Phyllodoce aleutica* (Spreng.) A. Heller, *Loiseleuria procumbens* (L.) Desv., and *Vaccinia*, especially *Vaccinium uliginosum* L. and *V. Vitis-Idaea*, make up part of the association, although quite often *Vaccinium* is completely lacking. Also found as members of the mat are *Campanula lasiocarpa* Cham., *Antennaria monocephala* DC., *Coptis trifolia* (L.) Salish., *Trientalis europaea* L. subsp. *arctica* (Fisch.) Hult., *Cornus suecica* L., *Linnaea borealis* L., *Veronica Stelleri* Pall. ex Spreng., *Cassiope lycopodioides* (Pall.) D. Don, and *Rubus stellatus* J. E. Smith. *Rubus Chamaemorus* L. is common in the western islands.

ROCK-CLIFF VEGETATION

At the bases of low-altitude rock cliffs there is usually to be found a seepage area with a rank growth of ferns, including *Athyrium*

Filix-femina (L.) Roth., *Cystopteris fragilis* (L.) Bernh., and sometimes *Botrychium* sp. and *Dryopteris Linnaeana* C. Chr. Also found here are *Claytonia sibirica* L., *Saxifraga bracteata* D. Don, *Selaginella selaginoides* (L.) Link, *Draba hyperborea* (L.) Desv., *Barbarea orthoceras* Ledeb., and *Saxifraga rivularis* L., the last being most common at higher altitudes in flat, wet-mud patches. Hultén thinks that *Barbarea* occurs only close to villages, but the writer has found it on uninhabited islands and in areas far inland from villages. Mosses of the wet cliffs include *Hylocomium splendens* (H.) Bry. eur., *Rhytidiadelphus loreus* (H.) Warnst., *R. squarrosus* (H.) Warnst., *R. triquetrus* (H.) Warnst., *Antitrichia curtipendula* (H.) Brid., *Drepanocladus uncinatus* (H.) Warnst., and others which occur regularly as part of the hillside-seepage vegetation.

WIND SLOPES

Beginning at no definite altitude is the very widespread alpine region of the Aleutians. It often extends down into the lower stream valleys and occurs close to the shore, although more commonly it is not to be found except inland. The entire vegetation is in an unstable condition. Major fluctuations have slowly occurred since the departure of the icecaps, which covered each island during the Pleistocene. Minor fluctuations continually occur today. They can be seen in the invasions, withdrawals, and reinvasions of certain plant associations, as, for example, in the shifting back and forth between marsh and meadow vegetation. Although longer than seasonal, these shifts are oscillatory and are brought about by periodic surpluses of moisture. Particularly heavy winter snowfalls often cause changes in areas from meadow to marshland, with a corresponding shift in vegetation. Many Aleutian plants show a surprising adaptability as well as capacity for invading newly available areas quickly. For example, Glacier Creek valley of Great Sitkin Island was visited by the author in 1949 and found to be choked with ice and snow. The newly ice-free areas were barren of plant growth. By the same time the following summer these areas were dotted with lichens, various mosses, sprouts of adventuring *Lupinus nootkatensis*, *Hieracium* sp., *Poa* sp., *Carex* sp., and a single *Campanula*. Hultén mentions the unusual pioneering ability of *Senecio Pseudo-Arnica*; it has invaded in numbers the famous Bogoslov Island, which has appeared above the sea, disappeared, and appeared again since

Russian times in the Aleutians. Hultén also observes that the Aleutian flora is largely the same as that of Kamchatka, with the addition of American elements throughout, but its associations are much less stable.

The alpine meadow is almost nonexistent, being merely a transition zone, usually narrow, between the lower or subalpine meadows and the alpine heath slopes above. *Calamagrostis Langsdorffii* (Link) Trin., *Geranium erianthum* DC., *Salix crassijulis* Trautv., *S. ovalifolia* Trautv., *Anemone narcissiflora* L., *Aster peregrinus* Pursh and other plants make up this transitional complex. Not infrequently the mountain-stream valleys consist entirely of this vegetation, with additional *Lycopodium* species, *Rhododendron kamtschaticum* Pallas, *Cornus suecica* L., and various short grasses and lichens.

The heath slopes of the island cover comparatively large areas and are truly the windswept, desolate, rocky, barren-appearing regions envisioned as typical of the Aleutians by most nonvisitors. Temperature differences between the coast and the inland heath slopes are sometimes fairly great, but apparently not so great as to cause large vegetational differences. It is, rather, that the high winds which constantly blow across the ridges and higher slopes of the interior are the primary factor in the vegetational make-up of these places. Despite the uniformly high humidities (85–95 per cent) in the Aleutians, the constant circulation of air caused by continual strong winds makes for desiccation of plant tissues. Hultén has appropriately called attention to the “wind planes,” areas over which the movement of the wind is not retarded by the relatively smooth surface of the greater part of the vegetation. Even a pocket in the vegetation a few inches deep is relatively out of the wind and therefore constitutes a considerably different microhabitat. I have chosen to call “wind slopes” those areas over which there is a “wind plane” at the general surface of the mat or heath vegetation, which has so profound a drying effect that it determines the aspect and form of the plant association. Where *Salix* is the only larger woody plant, it is procumbent, of “krummholz” form (Fig. 2).

Characteristically moulded by the wind planes are extensive areas of *Empetrum nigrum* L., *Cladoniae*, and *Salices*, which cover the ground as a weatherworn carpet. Many lichens and mosses make a part of this carpet, together with scattered growths of the following: *Lycopodium clavatum* L., *L. alpinum* L., *L. Selago* L.,

Carex rariflora (Wahlenb.) Smith, *C. circinnata* C. A. Meyer, *C. nigricans* C. A. Meyer, *Tofieldia coccinea* Richards., *Campanula lasiocarpa* Cham., *C. dasyantha* M. a Bieb., *Cassiope lycopodioides* (Pall.) D. Don, *Antennaria monocephala* DC., *Oxypetalum trifolium* (L.) Salisb., *Loiseleuria procumbens* (L.) Desv., *Calamagrostis purpurascens* R Br., *Linnaea borealis* L., various *Vaccinia*, and clumps of *Lupinus*



FIG. 2. Weathered trunk of a procumbent *Salix* (*S. crassifolia* Trautv ?) showing the usual "krummholz" form of plants subjected to high winds, including all the scattered willows in and above the *Empetrum* mat

nootkatensis Donn ap. Sims., and *Anemone narcissiflora* L. var. *villosissima* DC.

Within the heath zones are numerous moss- and lichen-covered boulders which have rolled from the eroding peaks and cliffs. Among the mosses of these special minute habitats are: *Hypnum callichroum* Brid., *H. Dieckii* R. & C., *Mnium punctatum* H., *Rhacomitrium aciculare* Brid., *R. lanuginosum* (H.) Brid., and *Pohlia cruda* (H.) Lindb.

Also characteristic of the windswept slopes in the interiors of the

Aleutians are eroded patches of gravel and rubble, which often form terraces of bare soil and rock on an otherwise heath-covered slope. Invading these highly unstable areas are scattered growths of *Polygonum viviparum* L., *Campanula lasiocarpa* Cham., *C. dasyantha* M. a Bieb., *Salix*, *Primula cuneifolia* Ledeb., *Antennaria* sp., *Barbarea orthoceras* Ledeb., *Cardamine umbellata* Greene, *Luzula nivalis* (Laest.) Beurl. var. *latifolia* Kjellm., *Petasites frigidus* (L.) Fries, and, less generally, *Oxyria* and *Saxifraga*. Pioneering lichens and mosses tend to invade first. The wind-eroded stems and roots of *Salix* present a picture like that of tangled diminutive beach driftwood protruding from sand, but the hardy willows manage to remain alive despite the windstorms and gravel blasting characteristic of these areas (Fig. 2). Other plants will grow when somewhat protected by the willows.

SPECIAL HABITATS

Inasmuch as the writer expects to treat such special habitats as steam jets, volcano craters, bird mounds, salt marshes, and village sites at a later date, they are passed over with mere mention in the present paper. Steam jets and hot springs have universally been disregarded by collectors in the Aleutians, but they possess a unique and interesting algal flora. They were used by the Aleuts as a source of ochres and, occasionally, for boiling food. In the steam of jets they placed strips of driftwood (*Taxus*) to be bent for the construction of boat frames. The writer made observations and collected algae and mineral specimens from such localities on Unnak, Kagamil, Atka, and Great Sitkin islands.

ALEUT CULTURE AND ALEUTIAN PLANTS

The Aleuts were well adapted to living along the peripheries of the islands, being almost exclusively a maritime people (Collins, 2). They seldom journeyed inland and did not seem to care much for higher ground. According to early Russian accounts, they were actually adapted physically more to paddling great distances cramped in skin boats than to walking even moderate distances overland. When they made trips into the mountains, they were usually in search of volcanic ochres and certain types of rock used in the manufacture of weapon points.

Their food supply was from either the sea or its margin. Aside

from sea mammals and fish, which comprised their main diet, abundant kelp, *Fucus*, *Ulva*, and small animals were gathered for food from the shore waters and reefs. Kelp was utilized in the making of fish lines. Along the shores grew species of *Senecio*, *Heracleum*, *Angelica*, *Claytonia*, *Cochlearia*, *Conioselinum*, *Achillaea*, and more than twenty other plants which were used extensively for food and medicine. *Lathyrus*, *Elymus*, and other grasses were employed in weaving. *Aconitum* was used by at least some of the Aleut villagers as a source of fish and whale poison. Although certain medicinal plants, such as *Matricaria*, *Caltha*, and *Menyanthes*, occurred chiefly in swampy areas, these were usually close at hand and did not necessitate a major trek inland. Berries were common in the lowland meadows. *Rubus*, *Vaccinium*, and *Empetrum* mats were thickest nearer the shore and thin at higher altitudes.

Soil depth and drainage, which were important considerations in the choice of sites for villages, were better along the shores of the islands than inland. From the sea came whale ribs, which were used as supports for the sod roofs of the Aleut barabaras. From the sea also came the Aleut's wood, for the only source was driftwood. From Asia he received as drift such woods as *Taxus cuspidata* S. & Z., which he bent into ribs for his boats. America contributed *Salix*, *Chamaecyparis*, *Taxus*, *Picea*, and other woods. The Aleut used cedar for masks; cottonwood for carving and, later, for smoking salmon; and birch for fashioning hats.

The sea not only furnished the Aleut with his livelihood, but also provided him with an avenue of escape from enemy attackers from neighboring islands. Even the flatest islands have raised portions near the beach which served as lookout posts for enemies and sea mammals. Caves, which were used for burials by at least some groups during a portion of Aleut existence among the islands, are far more common along the shores than inland. And were the Aleut to journey very far inland on his island, he would find the winds too violent for sustained comfort, and so he, like most modern visitors to the Aleutians, avoided the upland.

It would seem that the Aleuts were limited to their maritime existence by more than merely their cultural inheritance from a mainland source. That they were a maritime people prior to arriving in the Aleutians seems probable, but the Aleutian environment, with its climatic, vegetational, animal, and topographic limitations,

must have played no small part in the ultimate shaping of their way of life. Just how radically their customs were modified by the total impact of ecological factors remains, of course, indeterminable up to the present, but will to some degree be revealed, it is hoped, by the archaeological sequences in old village sites.

UNIVERSITY OF MICHIGAN

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Official U. S. Navy photograph

FIG. 1. Western tip of Attu Island, showing extremely mountainous terrain and rugged coastline common to the larger Aleutian islands. Although there are no active volcanos on Attu, these are a prominent feature of the eastern Aleutians.



Official U. S. Navy photograph

FIG. 2. Hak Island, an example of the Aleutian platform island. Such flat, usually small islands are found west of Adak. The vegetation of the central portion of the plateau is mainly *Empetrum* mat, which is surrounded by a narrow belt of meadow vegetation.



Crater lake on Kasatochi Island

Many ancient craters remain as evidence of past volcanism.

thirty-five active volcanoes on the Aleutian Arc

Official U. S. Navy Photograph

There are still approximately



FIG. 1. Stream ravine—wet and generally steep, with rank growth of ferns, grasses, and high-growing umbellifers.



FIG. 2. Lowland marsh, where commonly occur medicinal plants once used by the Aleut

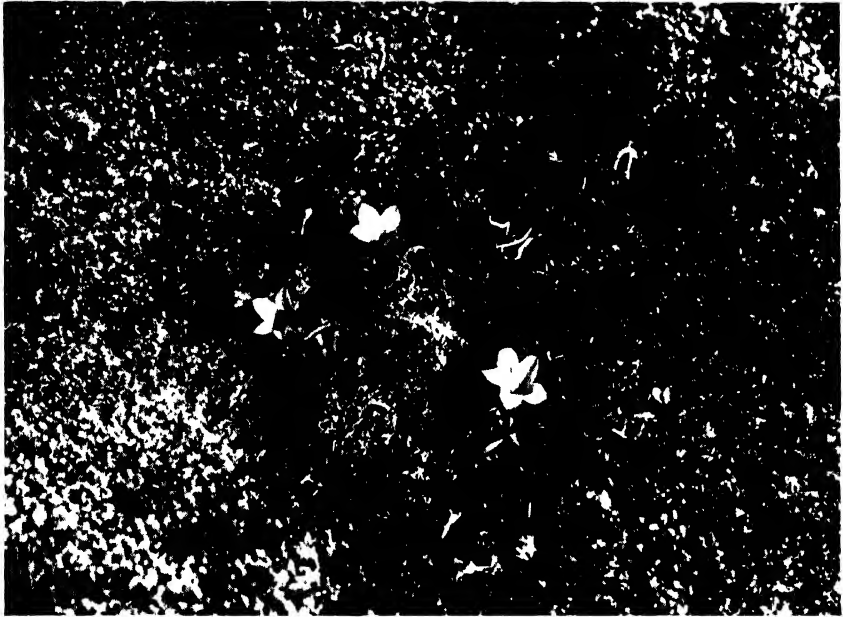


FIG. 1. Detail of an *Empetrum* mat. *Empetrum nigrum*, lichens, mosses, and a number of large-flowered plants, such as *Campanula* (shown), occur as part of this knoll and plateau plant association.



FIG. 2. Highland lake habitat, showing characteristic marginal stands of sedge.

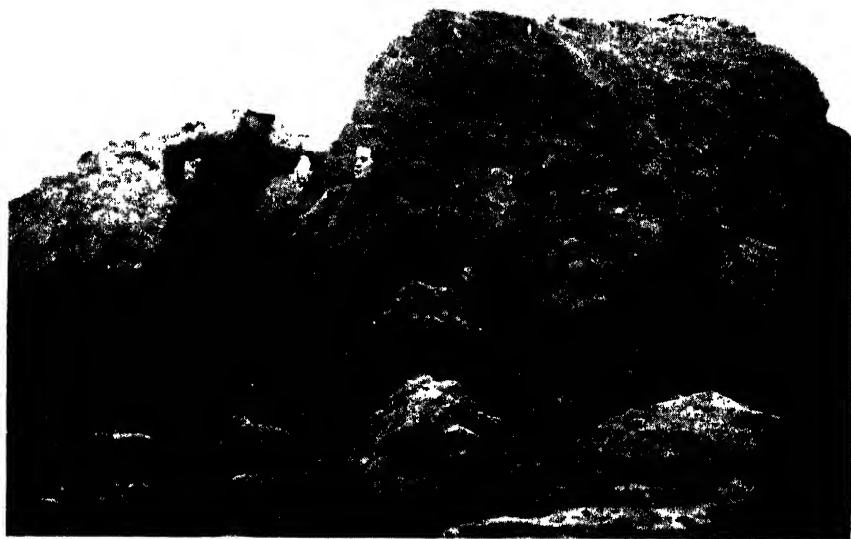


FIG. 1 Alpine mountaintop. Such heights are usually boulder strewn, with vegetation restricted by climatic factors, especially wind, mainly to lichens and mosses

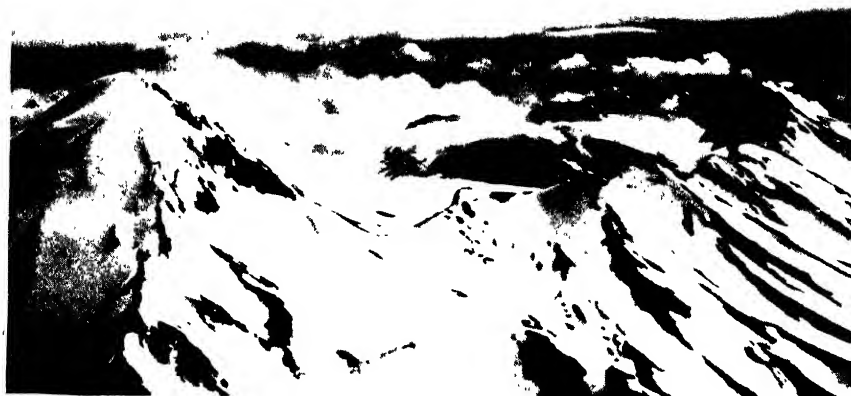


FIG. 2. Great Sitkin Volcano, July, 1948, an example of the physiognomy of many Aleutian peaks



FIG. 1. Bird mound. Such mounds are common along seashore cliffs throughout the Aleutians.



FIG. 2. Active steam jet near the sea, Kagamil Island, 1949

NATURAL REVEGETATION OF CERTAIN AREAS IN NORTHERN LOWER MICHIGAN FORMERLY COVERED BY BUILDINGS*

FRANK C. GATES

THE transfer of the University of Michigan Biological Station in Cheboygan County from the southeast side of Douglas Lake to the south shore of North Fishtail Bay in the winter of 1929-30 uncovered the sandy sites occupied by various buildings at the original location. Of the several available situations three were chosen to be set aside and fenced as preserves for subsequent study. They were sites that had been covered for short, medium, and long periods, as follows: the Research laboratory, three years, 1927-29; the Botany laboratory, six years, 1924-29; and the Houghton laboratory, sixteen years, 1914-29.

Both old and new sites are on soil designated as Eastport sand. It is a sand which had been developed and worked over when Douglas Lake was at a higher level. It has been exposed ever since the lake assumed its present level after the melting of the ice sheet. It is a rather sterile type of sand in which such plants as pines and blueberries grow but slowly. Being close to the level of Douglas Lake, it has a rather high water table which, however, is often disjunct from the surface. At the time of settlement the whole area was covered with pine. Logging, burning, and revegetation with the aspen association had taken place before the establishment of the Biological Station. A few seeding pines remained, however, and seedlings of pines were present here and there.

Each of the buildings was sledged bodily from its location to a center line and hauled away; thus no haulage occurred over any of the sites chosen for observation. All debris was cleared up during the winter of moving. On July 14, 1930, the areas chosen were fenced in and small creosoted stakes were put in to aid in mapping. Pictures have been taken in most of the summers since, and maps

* Contribution No. 514 from Department of Botany, Kansas State College, and a contribution from the Biological Station of the University of Michigan.

were made of the vegetation. We shall discuss the areas in turn, commencing with the one covered the shortest time.

THE RESEARCH LABORATORY SITE

The aspen trees on this area were cut early in 1927 and the sprouts mowed before the laboratory was built in the summer. The area covered contained about thirty-eight square meters. At the beginning of the summer of 1930 the outline of the laboratory was clearly marked on the ground (Pl. I, Fig. 1). During that summer the area became largely weed-covered, with an abundant influx of *Agropyron repens* from nearby grassy areas. Sprouts of *Populus grandidentata* and *Rhus glabra borealis* appeared and grew to a height of approximately a meter. Most of the twenty-four plants that appeared were annuals, largely of a weedy nature. Rosettes of *Verbascum thapsus* were present in greater numbers than any other species. In subsequent years aspens (*Populus grandidentata*) developed vigorously, reaching the largest number of shoots in 1933, after which through shading and competition the number was reduced to seventeen in 1939, thirteen in 1945, and seven in 1950. The increasing shade cast by an oak tree immediately outside the north boundary played a part in eliminating some of the aspens.

After five years of revegetation, controlled only by nature, the annuals were gone, except for one small plant of *Chenopodium album*, while the grasses and forbs which one associates with the aspens were present in such numbers and arrangement that, had one removed the fence, he would not have been able to outline the building. *Agropyron repens* and *Poa pratensis* were the main grasses to appear promptly. *Agropyron* spread in from the periphery by means of rhizomes, steadily becoming more abundant through 1935, after which it has been considerably thinned in the increasing shade. *Poa*, seeding in, reached its maximum in 1936. *Danthonia spicata*, *Poa compressa*, and *Panicum meridionale*, all normal to the aspens, have increased in number slightly as the years have passed.

Among the normal aspen forbs *Aster laevis* was present the first and second years, disappeared for two years, and since has been present in small numbers through the drouthy thirties. It has now increased to twenty-four plants. *Solidago hispida* appeared in 1933 as a single plant and barely maintained itself until the late forties.

It now has fifty-eight plants. The fern *Pteridium latiusculum*, so common in the aspens, represented by a single leaf the first year, made no showing until after the drouth. In 1950 thirty-one leaves were present. *Vaccinium angustifolium nigrum* first entered the area in the fourth summer and has increased but slightly. *Arctostaphylos uvaursi* appeared in the nineteenth year. Although an acorn-bearing oak (*Quercus borealis*) was just outside the area, no seedlings appeared until the fifth year, when forty-two were present. Many died. The number varied from year to year from a low of twenty-two in 1937 to a high of eighty-four in 1939 and 1940 (Pl. I, Fig. 2). Each year most of them die, but new ones come up. Very few are as much as five years old. *Acer rubrum* seedlings came in 1948, the nineteenth year. Nine are now present.

Pine cones were noted on the ground as early as 1933, but the first seedling to appear came in 1943 and a second in 1944. Both were growing slowly in 1950 (Pl. I, Fig. 3).

Mosses first appeared visibly in 1937, when *Ceratodon purpureus* invaded very sparingly in certain more open places. Moss has not made much progress in this area because of the excessive and nearly complete shade.

It has taken only five years to make up for the three years that plants were prevented from developing because of the presence of the building (Fig. 1).

THE BOTANY LABORATORY SITE

The Botany laboratory was built in 1924 in more open aspens, through the east half of which a sand road had been in existence for many years. The laboratory occupied about thirty-eight square meters of ground for six years before its removal. In the first summer after removal eighteen species made their appearance, all in modest quantities and most as single occurrences (Pl. II, Fig. 4). In subsequent years the number of species dwindled to eleven in 1938, since which time it rose slowly to nineteen in 1950. Aspens have not yet been an important element in the revegetation. Only since 1934, the fifth year, has any been permanent. There are now four, one of which is about 2 m. tall. Together they cast about one fifth as much shade on the area as a large aspen outside the tract to the south. All are *Populus grandidentata*. Moss, however, has

ABBREVIATIONS AND SYMBOLS USED IN FIGURES 1-4

Meter distances are marked along the edges of each plot.

Abbreviations of Specific Names

A	<i>Agropyron repens</i>
AC	<i>Acer rubrum</i> seedlings
AG	<i>Agrostis alba</i>
AM	<i>Amelanchier</i> sp.
AR	<i>Arabis lyrata</i>
AS	<i>Aster laevis</i>
ASC	<i>Asclepias syriaca</i>
AU	<i>Arctostaphylos uvaursi</i>
CB	<i>Carex bebbii</i>
CG	<i>Carex gracillima</i>
CH	<i>Chenopodium album</i>
CHR	<i>Chrysanthemum leucanthemum</i>
CI	<i>Cirsium pitcheri</i>
CO	<i>Comandra umbellata</i>
CU	<i>Carex umbellata</i>
D	<i>Danthonia spicata</i>
EA	<i>Erigeron annuus</i>
EC	<i>Erigeron canadensis</i>
EL	<i>Elymus canadensis</i>
F	<i>Festuca ovina</i>
G	<i>Geaster hydrometricus</i>
H	<i>Hieracium aurantiacum</i>
K	<i>Krigia virginica</i>
L	<i>Lepidium virginicum</i>
M	<i>Ceratodon purpureus</i>
MP	<i>Polytrichum juniperinum</i>
OE	<i>Oenothera muricata</i>
PC	<i>Poa compressa</i>
PM	<i>Panicum meridionale</i>
PP	<i>Poa pratensis</i>
PRP	<i>Prunus pennsylvanica</i>
PRV	<i>Prunus virginiana</i>

PT	<i>Pteridium latiusculum</i>
Q	<i>Quercus borealis</i>
R	<i>Rhus glabra borealis</i>
RO	<i>Rosa (blanda)</i>
S	<i>Solidago hispida</i>
SE	<i>Setaria viridis</i>
SJ	<i>Solidago juncea</i>
V	<i>Verbascum thapsus</i>
VA	<i>Vaccinium pennsylvanicum nigrum</i>
VI	<i>Vitis vulpina</i>

Other Abbreviations

CON	Concrete footing not removed (Figs. 3 and 4)
LVS	Leaves
O	Open ground, i.e. without plants
SP	Sparse
ST	Stump

Numbers

Numbers immediately before letters designating species indicate the number of plants found at the places indicated

Numbers not immediately before letters:

- 2 Very open sod
- 5 Open sod
- 7 Dense sod

Symbols

- *Populus grandidentata* (Figs. 1 and 2)
- *Populus tremuloides* (Figs. 3 and 4)
- ≡≡≡ Areas covered with dead leaves
- \\ Areas shaded at noon
- /// Areas of moss cover

(Pl. II, Fig. 6). The part of the area that had been a sandy road was the last part to become moss-covered. *Polytrichum juniperinum* first appeared in 1942 in small quantity in the masses of *Ceratodon* near the southwest corner and in the center of the south side.

Though this magnificent increase in moss cover did not cut down the total flora, it did materially lessen the number of individual plants to the point where the area now appears to be largely a bed of moss. The interstices are occupied by grass clumps rather than by sod grasses. *Danthonia spicata* was more common at first, but *Festuca ovina* increased much faster. Seedlings of *Rhus glabra borealis* appeared now and then, but only recently have they persisted. *Prunus pennsylvanica* does not establish itself. As the aspens in the area and those next to it grow larger and cast more shade, diminution of the moss carpet is to be expected, but meantime invasion of likely plants is greatly reduced.

Seeds of various plants studied in the laboratory dropped through the cracks in the floor. Some few grew in the first or the second season, such as *Chenopodium album*, *Epilobium angustifolium*, *Malva rotundifolia*, *Polygonum convolvulus*, *Polygonum persicaria*, *Rorippa hispida*, *Setaria viridis*, *Triticum aestivum*, and *Verbascum thapsus*. Most interesting of all, however, was the appearance the first year of a seedling of *Carex*, which the next year turned out to be *Carex gracillima*, a species normal to cedar bogs, here growing in open sand, wet season or dry season, very much out of habitat. Nevertheless it has persisted to the present time.

After the twenty-one years since this preserve was set up, it is still obvious just where the laboratory stood. As the shade of adjacent aspens and the few in the preserve gets denser, the area should become more and more an aspen area, as it had been (Fig. 2).

THE HOUGHTON LABORATORY SITE

Houghton laboratory was built in 1914 and covered about ninety square meters of ground for sixteen years. It was built on low pillars, so that the floor was not in contact with the sand. However, the edge of the building reached to the sand and thus shut off the light and prevented the development of plants underneath the building. With the removal of the building twelve species made their way into

TABLE I (Concluded)

Species	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1942	1945	1949	1950
<i>Acer rubrum</i>	1	2	2	1
<i>Erigeron canadensis</i>	4
<i>Ceratodon purpureus</i>	+	+	+	+
<i>Asclepias phytolaccoides</i>	2
<i>Rorippa</i> sp.	1
<i>Pteridium latiusculm</i>	5	14	8
<i>Solidago hispida</i>	(in 1948, 1)	..	1	1	1
<i>Prunus pennsylvanica</i>	(in 1948, 1)	..	1	..	4
<i>Polytrichum juniperinum</i>		+
	12	10	10	8	8	8	9	9	10	9	13	16	18	17	18

the area uncovered the first year, including at least five whose seeds probably came from activities in connection with the pressing of plants at the end of the building (Pl. III, Fig. 7). This area has been the slowest in revegetating, but has shown two lines of development. The earliest involved the spreading in from adjacent sand ridges of *Agropyron repens*, which came in the second summer and increased in density from year to year up through 1936 (seventh season), after which it decreased in density, although spreading in area somewhat. *Elymus canadensis* entered as two clumps in the first summer and increased during the next three years, since which time it has maintained a level of six to eight clumps. On the other hand, the sod grasses, *Poa compressa* and *Poa pratensis*, invaded promptly and increased year by year, reaching a maximum about 1938, but since then the accumulation of dead leaves has been instrumental in checking their normal extension.

At the west edge of the area aspens, here the tree *Populus tremuloides*, sprouted from the roots. The number of sprouts increased to a maximum in 1936, after which, although the number of stems diminished, the shade cast increased (Pl. III, Fig. 8). In 1950 there were twenty-six stems of *Populus tremuloides*, and 44 per cent of the area was shaded at noon. Two oak seedlings appeared in 1936, the seventh season. The number remained small through the drouth, but when wetter seasons came, the number reached seventy-four in 1942. At present (1950) it is forty-seven. Few of them live for more than a year or two. One *Acer rubrum* seedling appeared in 1942, a second in 1945, but only one poor plant remained in 1950. The common bracken fern, *Pteridium latiusculum*, although in the vicinity all the time, did not send rhizomes into the area until very late. Five leaves appeared in 1945, fourteen in 1949, and eight only in 1950 (Pl. III, Fig. 9).

Mosses first appeared in 1942, the thirteenth season, and have since increased in quantity, but are still very spotty in distribution, being kept in check by accumulations of dead leaves and increasing shade. The major species is *Ceratodon purpureus*, into whose areas a little *Polytrichum juniperinum* is now making headway.

This area, covered for sixteen years, shows by far the most open sandy appearance of all the areas. The revegetation had proceeded in greatest measure from the edges inward, instead of appearing all

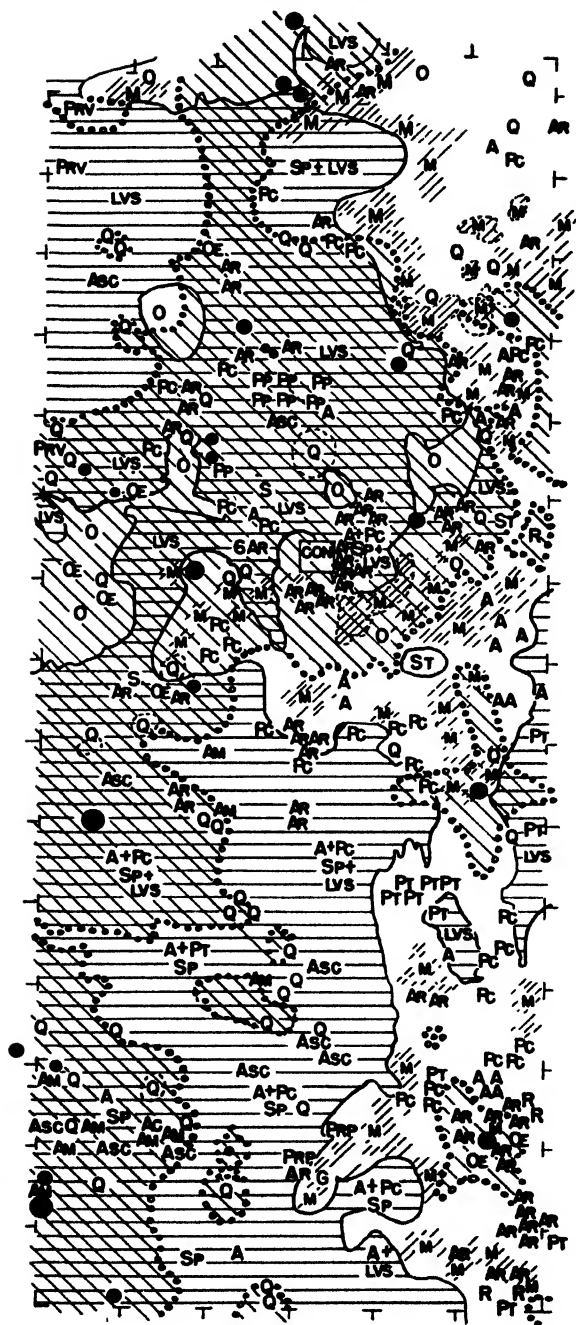


FIG. 4. Revegetation on the Houghton laboratory site in 1950

NUMBER OF SPECIES IN REVEGETATION

Areas of this size in the aspen association usually have between twenty and forty species of higher plants. Reference to Table II will show the number of species that have been present in the revegetation of these areas in the various years as indicated. The area covered for the fewest years witnessed the greatest number of invaders the summer after uncovering and has maintained a more varied flora ever since. The early development of trees furnished shade and kept the grass element from closing over the land with sod. It also prevented the moss, *Ceratodon purpureus*, from being an important factor in revegetation.

TABLE II

NUMBER OF SPECIES IN REVEGETATION OF SITES

(The figures give the number of species present in the years indicated.)

Years covered	Laboratory site	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1942	1945	1948	1949	1950
3	Research	24	22	14	16	17	18	18	19*	18*	23*	22*	20*	24*	20*	22*	28†
6	Botany	18	14	14	14	12*	13	14*	12*	10*	12*	12*	16*	16*	17*	14*	18†
16	Houghton	12	10	10	8	8	8	9	9	10	9	13	15*	17*	16*	16*	16†

* The asterisk indicates that the moss *Ceratodon purpureus* is also present.

† The dagger indicates that both *Ceratodon purpureus* and *Polytrichum juniperinum* are present.

The site of the Botany laboratory, covered for six years, was invaded by only three fourths as many species the first year, although there were a number of additional species in the immediate vicinity. Tree species were very slow in invading, and consequently the shade factor was minor during the twenty-one years. Until recent years nearly all the shade in the area was furnished by trees outside—never sufficient to be an important factor. The moss *Ceratodon* took advantage of this, even in the drouth years. With wetter summers this moss spread rapidly and eliminated many individual plants of several species, although it did not seem to cut down the total number of species in the area. The contrast between this area and that covered by the Research laboratory is very great.

The site of the Houghton laboratory, covered for sixteen years, has been by far the slowest in its revegetation. Only a dozen species

invaded it in the first summer, and four of these did not last into the fourth year. At first shade was from the edges, but it did not become important until after a dozen years had passed. Sod-forming grasses came in from the sides also, but were not very successful against the dead weight of leaves which accumulated and smothered them. Shade, accumulated dead leaves, and a little blowing sand relegated mosses to an unimportant rôle in the revegetation of this area. In a special plot not far away, but quite similar, spores of *Ceratodon* were sowed. In the five years that have since elapsed there has been no sign of moss plants. There is still more open sand in this area than in both of the others together. It is evident,

TABLE III
DISTRIBUTION OF SPECIES BY AREAS

Species in only one area			Species in two areas			Species in all three areas
Research	Botany	Houghton	Research Botany	Research Houghton	Botany Houghton	Research Botany Houghton
25	11	9	10	5	2	16
56%	24%	20%	59%	29%	12%	100%
45			17			16
58%			22%			20%
78						

however, that the effects of sixteen years' coverage are being overcome and that within another six or ten years the location of the laboratory will not be discernible to one who was not acquainted with the area in years past.

As will be seen from Table III, of the seventy-eight species concerned in the revegetation of these three areas forty-five, or 58 per cent, occurred in only one. Most of these were in the Research area, the area covered over the shortest time, to which twenty-five species, or 56 per cent, were limited. Sixteen, or 20 per cent of the seventy-eight species, were found in all three areas. Of these, thirteen, and probably fifteen, are typical plants of the aspen association. Only eleven of the species should be regarded as most unusual, and

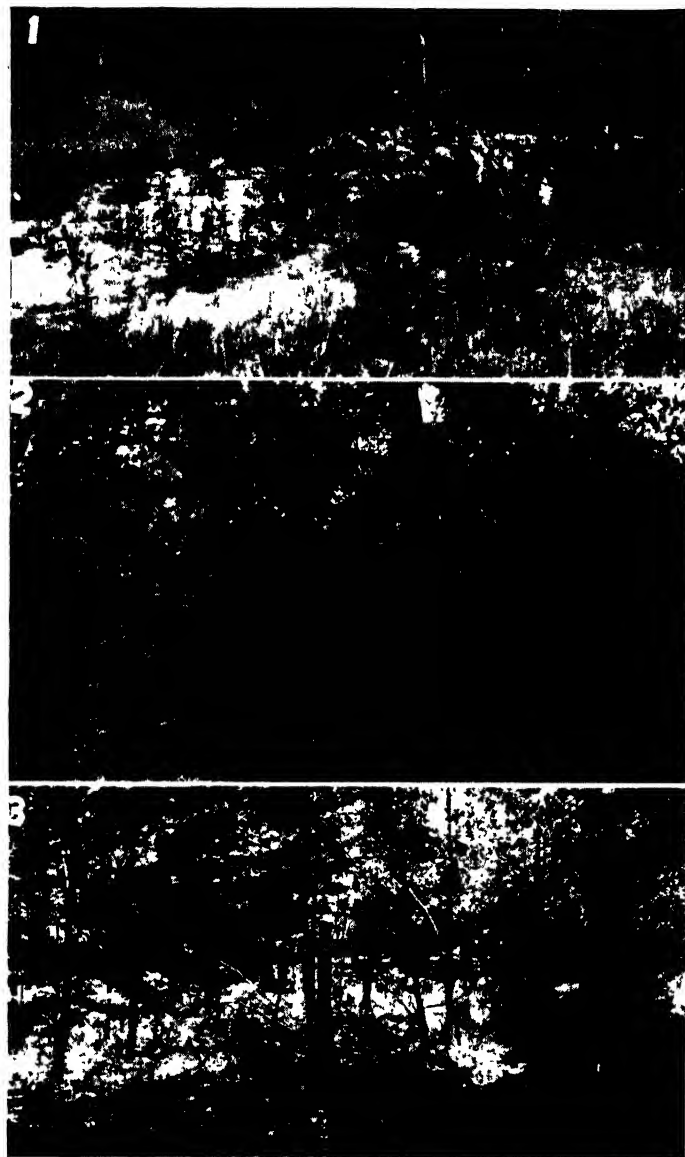
nine can easily be explained as having come from seeds that fell through the cracks in the floor to the sand below, one from the feed of the horses used in moving the buildings, and the eleventh from bird seed carried to experimental duck pens.

SUMMARY

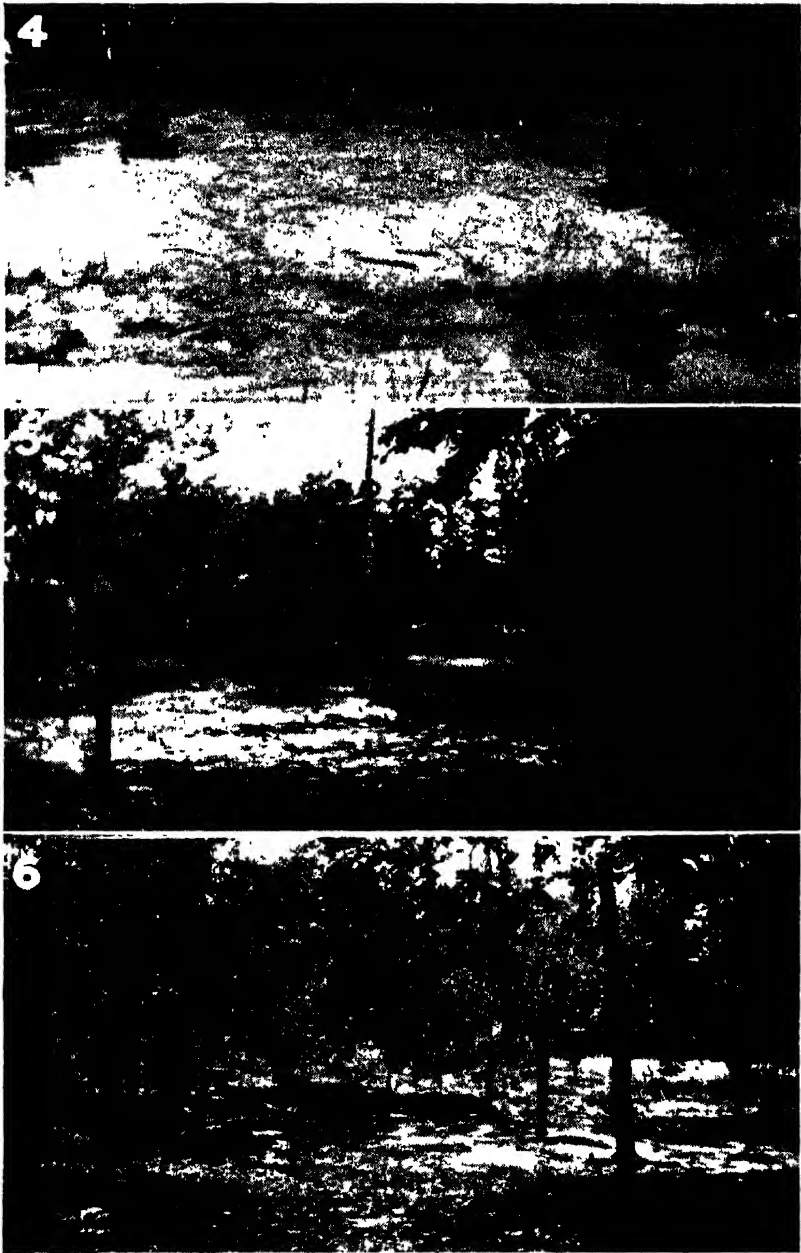
Areas covered over by buildings at the Biological Station of the University of Michigan for various periods of time have demonstrated that the longer an area is covered, the slower will be the natural revegetation, or, conversely, the shorter the time of coverage, the more quickly will the area be restored naturally to the appearance of the surroundings. Invasion of moss prolongs the restoration period.

KANSAS STATE COLLEGE
MANHATTAN, KANSAS

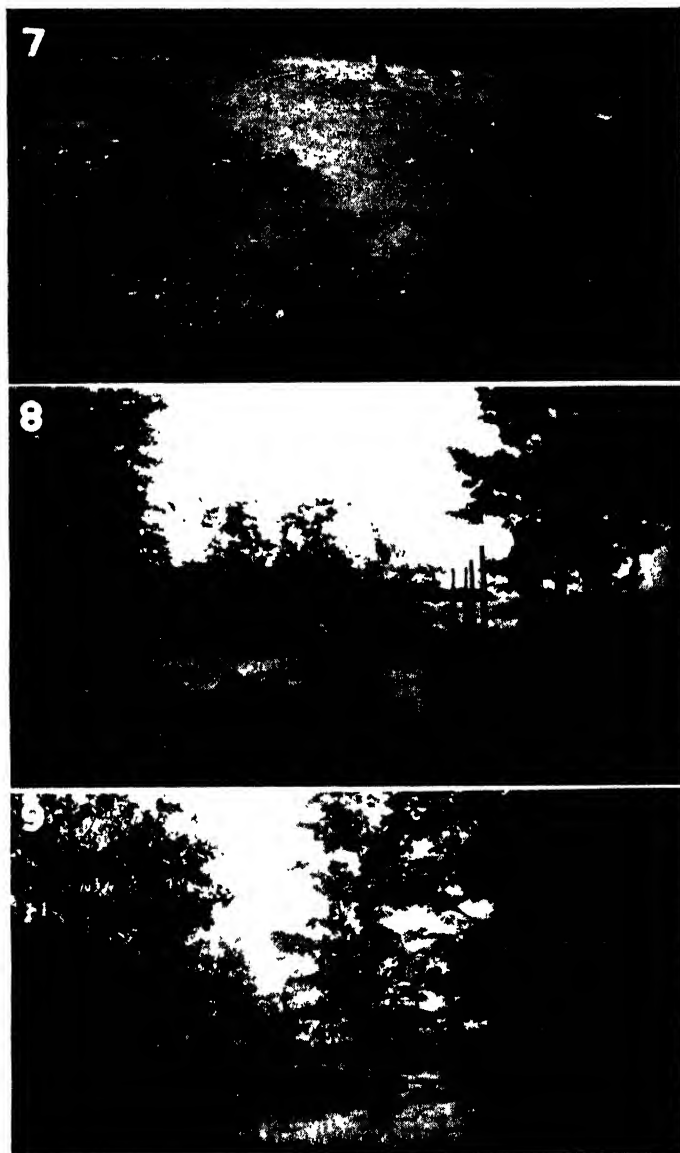
PLATES I-III



The Research laboratory site in 1930 (Fig 1), 1940 (Fig 2), and 1950 (Fig 3)



The Botany laboratory site in 1930 (Fig. 4), 1940 (Fig. 5), and 1950 (Fig. 6)



The Houghton laboratory site in 1930 (Fig. 7), 1940 (Fig. 8), and 1950 (Fig. 9)

A NEW STREPTOMYCES THAT PRODUCES VITAMIN B₁₂ ACTIVELY

KENNETH L. JONES

IT IS now well known that vitamin B₁₂ is produced by many soil microbes and that from them it is apparently absorbed by higher plants, which in turn supply it to animals. Since the commercial production of this important vitamin is feasible by mass-culturing of *Streptomyces*, the chain may be shortened by adding to animal feed crude vitamin preparations thus obtained. The new species here described, *Streptomyces vinaceus* (Jones), has proved to be useful in this regard.

Morphology.—Spore-bearing, aerial hyphae straight, monopodially branched and never producing regular spirals. Conidiophores irregularly septate with branches at the septa. Conidia spherical, oval, or even cubical, with a diameter of 0.4 to 1.0 micron, usually about 0.7. Length of the oval or cubical spores up to twice their diameter. Conidiophores slightly wider than the spores and much coarser than the substratal hyphae.

Gelatin stab.—No liquefaction. A buff-gray colony, 5 mm. in diameter, forms on the surface of the gelatin. It has a lobed margin and an irregularly folded surface. A thin layer of aerial hyphae develops over most of the colony. An extremely slight growth occurs along the line of inoculation. A dark-brown pigment diffuses throughout the upper half of the medium.

Gelatin plates.—No liquefaction. Colonies like those on stabs, but up to 12 mm. in diameter and oval. As with the stabs, they become sunken deeply below the original level of the medium and produce deep pits. A dark-brown ring of diffusible pigment 5 mm. wide surrounds each colony.

Plain agar plates.—Substratal mycelium forms a barely visible, colorless, effuse growth. Colonies 17 to 26 mm. in diameter, margin lacerate. No diffusible pigment. Aerial hyphae scanty and white.

Nutrient agar plates.—Colonies oval, about 11 by 15 mm. Substratal mycelium as viewed from lower surface, chamois¹ in color,

¹ The color terms are those of R. Ridgway, *Color Standards and Color Nomenclature* (Washington, D.C., 1912).

becoming cream buff at the periphery; the upper surface dark olive buff, fading to pale olive buff at the margin. Aerial hyphae occupy central portion of colony and are white to pale vinaceous fawn. No diffusible pigment.

Starch agar plates.—Colonies circular, 18 to 23 mm. in diameter. Substratal mycelium as seen from lower surface vinaceous buff to tilleul buff. Upper surface covered with aerial hyphae colored light vinaceous fawn, with numerous white sectors in every colony. No diffusible pigment. Starch digested in zones 5 to 8 mm. wide around each colony.

Calcium malate agar plates.—Colonies oval, usually about 10 by 15 mm. Substratal mycelium, as seen from lower surface, vinaceous buff, fading to colorless at periphery. Aerial hyphae on central 5 mm. area light vinaceous fawn. Remainder of upper surface cream color to colorless. No diffusible pigment. Calcium malate digested in a zone 0.5 to 4 mm. wide around each colony.

Bennett's agar plates.—Colonies oval, usually about 20 by 25 mm. Substratal mycelium as seen from lower surface russet or chestnut brown, center with irregular patches or concentric rings of lighter brown, the periphery a cinnamon buff. Sporogenous hyphae vinaceous fawn to Army brown, practically covering surface of colony. Diffusible pigment of cinnamon-buff color.

Potato plug.—Thick, finely wrinkled growth of substratal mycelium over the entire surface. This growth is cream-colored at the base of the slant but becomes brown and finally black in the upper portion. Aerial hyphae absent or barely visible; white. The potato is darkened in the upper portion of the plug.

Nutrient broth.—A ring of growth 3 mm. wide forms at the surface on the wall of a flask or tube. This pulls away and, if it floats, forms sporogenous hyphae. The broth is clear, forms a coarse sediment, and becomes alkaline (pH 8.6).

Litmus milk.—Milk becomes alkaline (pH 8.7). Cartilaginous ring of growth on tube as for nutrient broth.

Dextrose, sucrose, lactose, maltose, and mannite.—Growth with alkaline condition developing. No gas.

Nitrate reduction.—Positive but not carried on strongly.

Source.—Isolated from soil collections.

Habitat.—Probably soil.

Note.—Produces vitamin B₁₂.

SOUTHERN AND TROPICAL POLYPORES*

JOSIAH L. LOWE

MANY of the polypores, in common with other fungi, occur over a very wide area. Additional collecting in hitherto inadequately explored regions supplements records within the known ranges, and occasionally markedly extends the known distribution of rare and endemic species.

Very few monographs on the family Polyporaceae cover wide areas. Lloyd (1905-25) has treated certain genera for the world; Pilát (1936-42) has published a comprehensive manual for Europe, and Murrill (1907-08, 1914, 1915 a, b, c) has described the North American species.

The polypore flora of the southeastern United States presents a fascinating opportunity. The flora is now reasonably well known, but the distribution records are very incomplete. Two important papers have recently been published on the species occurring in the lower Mississippi Valley (Overholts, 1938) and in Florida (Murrill, 1947). Over several years Baxter (1934-50) has added much information on the resupinate polypores. Numerous papers of lesser scope have also appeared.

The plants in southern Florida and southern Texas merge with subtropical and tropical floras, and a number of typically tropical polypores are known to occur in these states. New elements may be expected. Two species hitherto unreported from the United States are included in this paper, and other specimens at hand, as yet unidentified, will add to this list. Many tropical polypores are known to have world-wide distribution. Comprehensive study in the southern United States inevitably brings the tropical polypore flora of the world under survey. Elements of South American and East Indian floras are well known from the work of Lloyd and Murrill, and I (Lowe, 1947, 1948) have recently reported a few examples. The tropical representatives in Central America and the West

* Contribution from the Department of Forest Botany and Pathology, State University of New York, College of Forestry, Syracuse, New York.

Indies are in need of critical study, and, particularly, the species described from tropical America need to be compared with the rich polypore flora of the East Indies.

The present paper, which is a report on collections of unusual interest made in the summers of 1949 and 1950,¹ records a marked extension of the known ranges of *Polyporus spathulatus*, *P. subcartilagineus*, and *P. tepeitensis*; it supplies additional taxonomic information on *Fomes taxodii*, *Polyporus fissilis*, and *P. floriformis*; and *Polyporus submurinus* is placed in synonymy with *P. meliae*.

Polyporus spathulatus (Hook.) Fries

This species is reported by Murrill (1915 b, p. 73) as frequent throughout tropical America. Although no collections in the United States have hitherto been reported or seen, numerous specimens were collected on the ground in early September, 1950, near Homestead, Florida. The fruiting body appears like small multiplex specimens of *Polyporus cinnamomeus* Jacq. ex Fries. The upper surface is a beautiful silky-yellowish brown, but the very minute pores, about 10–15 per mm., readily distinguish it from all other similar stipitate brown species, which have very much larger pores, 1–4 per mm.

The spores, not previously described, are brown, smooth, broadly ellipsoid, $2.5\text{--}3 \times 1.5\text{--}2 \mu$. The hyphae are abundantly septate as in *Polyporus cinnamomeus* and similar species, but narrower, 3–4 μ , rarely 5 μ , in contrast to a diameter of 4–7 μ in all the similar species.

Polyporus subcartilagineus Overh.

Only three collections of this species have been reported, two from Quebec and one from Pennsylvania. The species is, however, rather common in the Adirondack Mountains of New York, and is also common in the high-mountain country of western North Carolina and the Great Smoky Mountains of eastern Tennessee. It has been and very readily is confused with *Polyporus fragilis* Fries. In the fresh condition the context tissue next to the substratum is translucent and rather crisp (not watery); this is a good field characteristic. Certain distinction, however, turns upon differences in the

¹ In 1950 I was in the employ of the Division of Forest Pathology, Bureau of Plant Industry, Soils and Agricultural Engineering, United States Department of Agriculture.

spore shape. In *P. subcartilagineus* the spores are short-cylindric, $4.5-6.5 \times 2-3 \mu$; in *P. fragilis* they are slender, allantoid, $4-5 \times 1-1.5 \mu$.

The rot associated with *P. subcartilagineus* is of the brown cubical type.

***Polyporus tepeitensis* (Murr.) Lowe, comb. nov.**

This species was described (Murrill, 1912, p. 142) from three collections made near Cuernavaca, Mexico. No additional collections appear to have been made until very recently, when abundant material was found on sassafras, black locust, and sumach near Gatlinburg, Tennessee, in the Great Smoky Mountains National Park, always on standing small trunks or limbs some distance above the ground.

Some distinctive features of this plant are not included in the original description. The hyphae are nonseptate, solid, $1.5-2.5 \mu$ in diameter, and the spores are hyaline, smooth, broadly oval, $5-6 \times 5 \mu$. These microscopic characters readily separate the species from immature specimens of other species of similar external appearance, for example, *Polyporus ectypus* Berk. & Curt., *P. hollickii* (Murr.) Lloyd, *P. semisupinus* Berk. & Curt., and *P. subectypus* (Murr.) Bres.

***Fomes taxodii* Murr.**

This species, described from sterile material collected on *Taxodium* in northern Florida, was found rather frequently in fertile condition on the same host in the Okefenokee Swamp in Georgia in 1950. The spores are hyaline, smooth, broadly ellipsoid, $4.5-5 \times 2.5-3 \mu$. Type material, kindly loaned by Dr. W. A. Murrill, had setae, as did my own collections, although they were said to be absent in the original description (Murrill, 1938, p. 651). The setae are subulate, $20-30 \times 6 \mu$.

***Polyporus fissilis* Berk. & Curt.**

This species frequently occurs in a nodular condition in Georgia and northern Florida and is then indistinguishable in the field from *Polyporus compactus* Overh. The chlamydospores afford ready separation. In *P. fissilis* they are ovoid, $5-7 \times 3-5 \mu$; in *P. compactus* they are larger, $8-11 \times 7-9 \mu$.

Polyporus floriformis Quél.

A collection (Lowe, 4483) made in western North Carolina on *Liriodendron* appears to be the second report of this species on a hardwood substratum. Zeller (1922, p. 182) has previously reported it on maple from Oregon.

Polyporus meliae Underwood

The type of this species is represented by two specimens in excellent condition, both with the annual growth typical of the genus *Polyporus*. The species was transferred to the genus *Fomes* by Murrill (1903, p. 232) for reasons not now apparent, as there are no specimens in the New York Botanical Garden that support the transfer, and no such material has been seen elsewhere. Occasionally, as in several other species of *Polyporus*, the fruiting body may revive and form a second, poorly developed, layer of tubes.

Its supposed perennial nature has, among other characteristics, served to separate this species from *Polyporus submurinus* (Murr.) Lloyd. On direct comparison of the type material of both species it became clear that the growth habits of the two differ somewhat, but the internal microscopic details, in particular the hyphae and the hymenial elements, agree exactly. *Polyporus submurinus*, therefore, should be relegated to synonymy under the earlier valid name, *P. meliae*.

Lloyd (1905-25, 4: 283) believed that this species was synonymous with *Fomes connatus* (Weinm.) Gill. Externally the type of *Polyporus meliae* closely resembles the first year's growth of *F. connatus*, but internally the two species are entirely dissimilar.

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STUDIES IN PLANT CARBONIC ANHYDRASE*

I. OCCURRENCE, DISTRIBUTION, AND PROPERTIES

EUGENE H. LUCAS AND RICHARD U. BYERRUM

AT THE annual meeting of the Michigan Academy of Science, Arts, and Letters in 1948 the senior author presented a paper entitled "Preliminary Report on Carbonic Anhydrase in Plants." It recorded the occurrence of carbonic anhydrase in the leaves of more than thirty species of phanerogams. At that time the senior author was unaware of a paper by Bradfield (3), published in 1947, which essentially had shown what the preliminary report was supposed to show, namely, the wide occurrence of carbonic anhydrase in leaves of green plants. Until Bradfield's paper appeared several contradictory statements had been published on this subject (2, 3, 5, 6). The senior author's paper thus confirmed Bradfield's finding that carbonic anhydrase could be generally detected in photosynthetic tissue provided adequate techniques were employed.

Shortly before the present material was assembled an extensive study was published by Waygood and Clendenning (7) which in many respects coincides with the subject of this paper. Apparently work on plant carbonic anhydrase was conducted independently by both the Canadian group and the Michigan State College group at the same time. The main results and conclusions are in agreement.

OCCURRENCE IN PLANTS

It can now be assumed that the existence in the leaves of green plants of an enzyme which catalyzes the reversible reaction $\text{CO}_2 + \text{H}_2\text{O} \rightleftharpoons \text{H}_2\text{CO}_3$ is an established fact. The main incentive for a search for plant carbonic anhydrase has been its possible connection with photosynthesis. This possibility was first suggested by Burr (2), but was ruled out on the basis of experimental evidence and theoretical considerations. The results obtained by several investigators (1, 3, 6, 7) have shown a rather wide range of activity. Although each

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worker or group of workers has used a different way of expressing enzyme activity, it has become apparent that there are some plants with high activity and others with very low activity. Several environmental factors, however, play a role in the enzyme activity measured under various conditions. Waygood and Clendenning (7, 8) express enzyme activity in a manner similar to that of Meldrum

TABLE I
PLANT CARBONIC ANHYDRASE ACTIVITY IN LEAF EXTRACTS OF SOME SPECIES
OF PLANTS

(e. u. = enzyme units)

High activity (over 80 e. u.)	Medium activity (between 20 and 80 e. u.)	Low activity (below 20 e. u.)
Species		
Tulipa Gesneriana	Medicago sativa	Triticum vulgare
Polygonum persicaria	Cucumis sativus	Rumex crispus
Rubus strigosus	Phaseolus vulgaris	Arachis hypogaea
Raphanus sativus	Antirrhinum majus	Daucus carota
Capsicum annuum	Chrysanthemum hortorum	Matthiola incana
Chenopodium album	Dianthus caryophyllus	Hydrangea paniculata
Brassica oleracea		Vinca minor
Pisum sativum		Lycopersicon esculentum
Lathyrus odoratus		Cyclamen persicum
Phaseolus lunatus		Allium cepa
Gypsophila paniculata		Cytisus genista
Lupinus angustifolius		Urtica dioica

and Roughton (4) in their pioneering work on animal carbonic anhydrase. An enzyme unit is used which is derived from the ratio $\frac{R-R_o}{R_o}$, where R equals the rate of catalyzed dehydration and R_o equals the rate of uncatalyzed dehydration in a given time. In earlier work the authors also used this ratio. It was soon found, however, that for comparative measurements the ratio is inadequate. Meldrum and Roughton dealt with a single material, blood, whose composition was very uniform. Plant extracts vary considerably in dry matter, and it was therefore considered necessary that the ratio express this variation. For this reason the ratio $\frac{R-R_o}{g}$, in which g equals weight in grams of dry matter, was substituted.

Table I compares the activities of a number of species tested. In order to take into consideration variations owing to environmental conditions the results were summarized after at least ten tests of each species at different times of the year, under different growing conditions and at different ages. These tests have given occasional overlapping of enzyme values, and it was therefore thought advisable to arrange the species in three groups, representing high, medium, and low enzyme activities. In each case the activity was determined manometrically. The shaking of the enzyme solution and substrate took place in a water bath of 30° C. The shaking unit was fitted with

TABLE II
COMPARISON OF CARBONIC ANHYDRASE ACTIVITY IN LEAVES
AND OTHER GREEN PARTS OF PHASEOLUS VULGARIS AND
CHENOPODIUM ALBUM

Species	Leaves	Stems	Stems and petioles
	Enzyme units		
<i>Phaseolus vulgaris</i>	70	14	
<i>Chenopodium album</i>	105	.	26

an Erlenmeyer flask with divided bottom. The rate of shaking was 120 oscillations per minute. Since mixing was found to be uniform from the outset of shaking with negligible variations, the measurements were started at zero time. Two milliliters of 0.2 M phosphate buffer of pH 6.8 and 2 milliliters of 0.1 M sodium carbonate in 0.01 M sodium hydroxide were used as substrate. One-half to one milliliter of enzyme solution was added, according to the concentration and activity of the material. The activity was determined by subtracting the uncatalyzed rate (boiled control) from the catalyzed rate and was expressed in micromoles, per gram of dry weight, of CO₂ evolved in thirty seconds. The values thus obtained are enzyme units (e. u.).

The enzyme seems to be present in all plant parts participating in photosynthesis. Internodes of kidney beans, and stems and petioles of lamb's-quarters were found to have definite, though low, activity (Table II).

It is interesting to note that low activity was also established in a species of *Euglena* grown in a rice-wheat medium. In most plants the older leaves have higher enzyme activity. Table III

shows that leaf age is not necessarily correlated with activity. While tulip leaves, for example, were less active when young, mature leaves of snapdragon were less active than young ones.

LOCALIZATION IN THE CELL

The work of Waygood and Clendenning (7, 8) has clarified the question of intracellular localization. They showed that a single high-speed centrifugation of the leaf extracts left only 2 to 50 per cent of the carbonic anhydrase activity in the chloroplast fraction. Washing with water removed an additional part of the activity from the chloroplasts (7).

TABLE III
PLANT CARBONIC ANHYDRASE ACTIVITY IN RELATION TO
AGE OF LEAVES

Species	Age of leaves	Enzyme units
Tulipa Gesneriana	Mature	104
	Young	48
Antirrhinum majus	Mature	26
	Young	40

These findings have been in general confirmed in the experiments of the authors. Since the first separations were performed by a method similar to that used by Meldrum and Roughton (4), this result was somewhat unexpected. Meldrum and Roughton, using ox-blood corpuscles as the source of enzyme, shook a water-ethanol suspension with chloroform and then centrifuged. They obtained a top layer of enzyme solution, a central layer of denatured protein, and a bottom layer of chloroform (4). When water extracts of leaves were subjected to a similar treatment, the main activity invariably resided in the supernatant liquid. A flocculate, which occasionally formed, and the chloroplast fraction showed considerable activity at first. This activity, however, was quickly lost on storage, whereas that of the supernatant remained stable for some time (Fig. 1).

PROTECTIVE AND INHIBITING PRINCIPLES

It was pointed out in the paper presented at the Academy meeting in 1948 that the apparent absence of the enzyme in certain plants

may be due to the inability to retain the activity in the extract. Any destructive agent which might come in contact with the enzyme

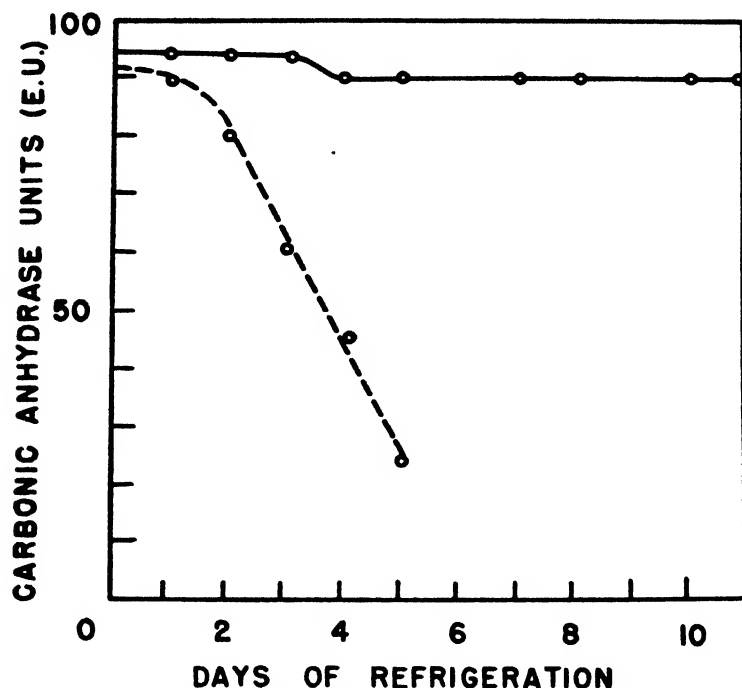


FIG. 1. The rate of degradation of carbonic anhydrase activity in the supernatant (solid line) and the chloroplast fraction (broken line) of centrifuged leaf extract of *Pisum sativum* held in a refrigerator

TABLE IV
THE RETENTION OF CATALYTIC ACTIVITY IN LEAF EXTRACTS
AFTER BOILING

Species	Fresh extract	Boiled extract
	Enzyme units	
<i>Tulipa Gesneriana</i>	115	15
<i>Pisum sativum</i>	96	7

during the process of maceration could be responsible for it. Waygood and Clendenning, who also investigated this possibility, did not find an inhibiting effect of tomato-leaf extracts, which have very low

enzyme activity, on parsley-leaf extracts when blended with them (7). As reported in 1948, tomato-leaf extracts showed an increase of activity when boiled pea-leaf extracts were used in their preparation instead of water. It was assumed then that a protective substance contained in the pea leaves but absent in tomato leaves might have been responsible for this phenomenon. In the light of the present studies it seems more likely that this effect is due to the weak activity

TABLE V
STABILITY OF CARBONIC ANHYDRASE IN PLANTS FROZEN AFTER HARVEST
AND STORED AT -5° F.

Species	Fresh leaves	Stored six months	Stored one year	Stored two years
	Enzyme units			
<i>Tulipa Gesneriana</i> ..	120	124	125	120
<i>Chenopodium album</i> ...	110	110	105	105

TABLE VI
STABILITY OF CARBONIC ANHYDRASE EXTRACTS AT 0° F.

Nature of extract	Freshly prepared	Stored for five months and thawed
	Enzyme units	
<i>Chenopodium album</i> leaves blended with three times their fresh weight of water	87	80

of a heat-stable catalyst in the pea leaves. It has been observed that the heated controls of some leaf extracts still retain weak activity (Table IV). For this reason boiled controls were used in most of the experiments instead of water controls in order to determine the enzyme activity.

STABILITY

In general, the enzyme activity has been found to diminish rapidly. Some leaf extracts, however, for instance, those from tulip and lamb's-quarters, retained activity over a remarkably long period.

Both materials were frozen and stored for periods of several months to two years at temperatures of 0° F. and below and did not lose much of their enzyme activity (Tables V and VI).

SUMMARY

1. The general occurrence in green tissues of phanerogams of an enzyme catalyzing the dehydration of carbonic acid is reported.
2. Similar enzyme activity could also be detected in the photosynthesizing protozoon *Euglena deses*.
3. Plant species have a well-defined level of activity ranging from high to very low.
4. The enzyme activity is located in the cytoplasm.
5. At temperatures below 0° F. enzyme activity is retained to a considerable extent in the plants as well as in extracts.

This work will be published elsewhere in greater detail.

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A PRELIMINARY ACCOUNT OF OENOTHERA TYPES IN THE KEWEENAW PENINSULA OF MICHIGAN

CHARLES D. RICHARDS

DURING the summers of 1949 and 1950 I critically botanized localities in the Keweenaw Peninsula of Michigan with the purpose of subjecting to a test M. L. Fernald's conclusion that that area was a refuge for plants during the last glacial period. Even if his hypothesis in unmodified form is not acceptable, there is at least a possibility that parts of the Keweenaw Peninsula sustained vegetation a considerable time before the general melting of the ice, and such a modification of the hypothesis might possibly explain some of the peculiarities of distribution of certain plants. In the course of the work special attention was directed to *Oenothera* because of the diversity shown by this remarkably variable genus.

In this paper there is no speculation about the relative antiquity of the various types that were found to be distinguishable. It is clear, however, that the localities of plants of disjunct distribution, like West Bluff, were not remarkable for diversity or unusual localization of their *Oenothera* flora.

I am not attaching names to the various distinguishable entities because, as this article is being written, it is reported that Professor R. E. Cleland has in press a book dealing with the *Oenothera* problem, and Professor R. R. Gates has a revision of this genus ready for publication. These works are expected to present much of the previous investigation in better perspective than does anything now in print.

It would needlessly complicate the situation to publish with names a detailed account of the distinguishable types of one small region. It will help to indicate roughly the characteristics by which the *Oenothera* population of a restricted area can be classified into entities that are genetically distinct. I have not tested these plants by garden cultures, but the distinctive traits are such as have been found by several workers to breed true with extraordinary constancy.

In keying out distinguishable entities I do not consider it necessary to go to the ultimate degree of subdividing, and at the moment I see no need for long descriptions. On the contrary, I present a key which in the main provides contrasting features that can be distinguished after one attains reasonable familiarity with the group. Types may be named later if they do not fall reasonably well into the categories provided in the forthcoming works of Cleland and Gates.

Since no names are here assigned, there is no need to worry about what represents a species, a variety, or a form in the Keweenaw flora. For the present it is sufficient to indicate that in two field seasons devoted no more intensively to *Oenothera* than to several other critical genera, twenty-one distinguishable entities turned up, and various others that were not in proper condition for study. The number is about what one would expect in view of earlier and almost entirely unpublished studies by H. H. Bartlett and others. These studies indicate that in any locality containing more than one genetic entity there will probably be four or more others, since the phenomena of twin hybrids and of mixed patrocliny and matrocliny are likely to give at least four types from each two distinct basic types. If a locality has more than six types, it is to be expected that some will not be distinguishable from the standpoint of practical systematic botany.

As for the method of attacking such a complicated problem, it is interesting to consider what each locality and habitat provides in the way of systematic entities that would unquestionably have nomenclatural status if they had any determinable geographic range. The distinguishing of genetic or, at least, systematically satisfactory types over a reasonable geographic range is now one of the greatest difficulties that confronts the botanist who is not willing to throw a medley of distinguishable genetic entities together under a single name that has no significance either geographically or biologically.

I have, therefore, made somewhat of a departure in *Oenothera* literature by keying out everything that I could from a geographically natural region, and then indicating the expectations for single localities and habitats.

The Keweenaw Peninsula, which is the geographical region under consideration, projects into Lake Superior in a northeasterly direction from the main part of the Northern Peninsula of Michigan. It is approximately 65 miles long, 28 miles wide at its southern end, and about 2.5 miles wide at its northern tip. Parts of three counties are

included within its boundaries, namely, Keweenaw, Houghton, and Baraga. Although much of the peninsula is forested and unsuited to maintaining populations of *Oenothera*, there are numerous places that offer excellent habitats for these plants, which prefer a disturbed soil. Such habitats are found on the sandy and gravelly beaches, on old mine sites, in abandoned quarries and fields, along roads and railroads, and around sawmills and lumbering camps. An attempt was made to visit as many of these kinds of localities as possible and to make critical collections from the *Oenothera* population present.

An enumeration of these localities follows, with a brief description of the habitats and of the *Oenothera* types found in each.

KEWEENAW COUNTY

1. *West Bluff*

• West Bluff was made famous by Professor Fernald, who considered it a nunatak refuge for plants during the maximum Wisconsin glaciation. It extends in an east-west direction parallel to the shore of Lake Superior. At its highest point it rises 735 feet above the lake level. The north side of the bluff slopes gently toward Lake Superior and is covered chiefly by young aspen stands with many grassy openings. The south side of the bluff consists of deeply weathered trap and conglomerate cliffs with a well-developed talus slope, which merges into the forest of the valley. The rim of these cliffs, which is constantly being swept by a strong wind blowing up from the valley, consists of rotted conglomerate and presents a bleak habitat for plant life. Three collections of *Oenothera* were made on the barren summit of these cliffs. These were associated with species which Fernald considered preglacial relicts, namely, *Chamaerhodos Nuttallii* var. *keweenawensis*, *Ceanothus sanguineus*, *Carex Rossii*, *Woodsia oregana*, and *Potentilla pensylvanica*.

It is to be presumed that, if Fernald's hypothesis is true, any localized *Oenothera* might conceivably be added to the relict group, and particular attention was therefore given to securing representative material of whatever was there. It turned out that only one distinguishable type was present, which was not highly localized, being found at other localities which were never considered nunataks. Of course, since *Oenotherae* are of definitely weedy propensities, there is no reason why the range of nunatak relicts might not have become extended even somewhat erratically, since the forest was widely cleared.

The single *Oenothera* type, which was collected under numbers 1043, 2443, and 3789, has the following distinguishing characters: calyx tips subterminal; inflorescence declinate when young; ovary not conspicuously red-papillate; hypanthium yellow; ovary very densely and hypanthium densely viscid-pubescent, both also pilose but with no visible crispate short pubescence among the pili.

2. *Phoenix Mine*

This locality presented an artificial habitat on which the sampling of the *Oenothera* population indicated the presence of only one type. The abandoned copper mine produced a hilly gravel dump on which the vegetation was very meager, so that the soil was not fixed, and not many species are successful invaders. The single *Oenothera*, collected under number 2052, was somewhat depauperate but healthy, and belonged to the *litorea* assemblage. Its distinguishing characters are as follows: calyx tips subterminal; inflorescence declinate when young; ovary not conspicuously red-papillate, almost lacking viscid pubescence, but with dense crispate pubescence among the pili; hypanthium yellow, only moderately viscid-pubescent.

3. *Great Sand Bay*

This locality is about two miles east of the village of Eagle River. It is a broad bay with a pebbly beach and steep sand dunes behind the beach. An attempt has been made to arrest the shifting dunes by planting pines and beach grass. Conspicuous native pioneers on the dunes are *Lathyrus japonicus*, *Artemisia caudata*, and *Oenothera* sp. At this locality the constant shifting of surface soil, so conducive to the multiplication of *Oenotherae*, comes about from erosion and redeposition by wind.

The single *Oenothera* type was collected under numbers 2770 and 3806. It can be distinguished from other members of the group by the following characters: calyx tips subterminal; inflorescence declinate when young; ovary conspicuously red-papillate; hypanthium red. In the last characteristic it resembles *O. perangusta* var. *rubri-calyx*, recently described from the Thunder Bay District, Ontario, by Gates.¹ It differs from Gates's plant, however, in having the ovary conspicuously red-papillate.

¹ Gates, R. R., "Another Parallel Mutation in *Oenothera*," *The Canadian Field-Naturalist*, 64 (1950): 142-145.

4. *Eagle River*

This is a locality on the north shore of the Keweenaw Peninsula. Two collections of *Oenothera* were made here, which proved to be different. No. 4832 was growing on the sandy beach along Lake Superior and No. 4375 along the road at the edge of the village. Their distinguishing features are as follows: (1) 4832: calyx tips subterminal; inflorescence declinate when young; ovary not conspicuously red-papillate; hypanthium red. This may correspond to *O. perangusta* var. *rubricalyx* of Gates. (2) 4375: calyx tips subterminal, 0.5 to 1.0 mm. long; inflorescence not declinate when young; ovary not conspicuously red-papillate, densely gray-pubescent.

5. *Bete Gris Bay*

This large bay is located on the south side of the Keweenaw Peninsula near its tip. The beach is sandy and flat, and the dominant vegetation consists of red pine. On the open beach *Hudsonia tomentosa*, *Lathyrus japonicus*, *Prunus pumila*, and *Oenothera* sp. were among the most prominent plants. The *Oenothera* population appeared to be quite uniform, so that only a single collection was made, number 3684. Its distinguishing characters are: calyx tips subterminal; inflorescence declinate when young; ovary conspicuously red-papillate; hypanthium yellow; ridge at back of bract with red papillae extending onto it from stem ridge.

6. *Mandan*

This locality is a ghost town about five miles east of the present village of Delaware. The houses of the old mining town are still standing, but for many years the yards and gardens have yielded nothing except large crops of weeds. *Oenothera* has found a suitable habitat here, but diversity in the population is apparently not great, since only one distinguishable type was found. It is number 4431 and can be defined as follows: calyx tips terminal; ovary conspicuously red-papillate; bracts shorter than the buds; bud cone and hypanthium yellow.

This type was found at many other localities, and it is undoubtedly the most common one on the peninsula.

7. *Lake Upson*

This small lake is located at the western end of West Bluff, and the *Oenothera* population here consisted of several colonies along the road to the north of the lake. The single collection bears number 3797 and is not readily distinguishable from Mandan 4431.

8. *Fort Wilkins*

This old fort, now reconstructed and preserved in a state park, is located one mile east of Copper Harbor not far from the northern end of the peninsula. *Oenothera* is by no means a conspicuous element in the flora around the fort, but occasional plants were found in disturbed soil. A single collection, 2522, appeared to belong to the same type, which proved to be, for all practical purposes, identical with Mandan 4431.

HOUGHTON COUNTY

1. *Houghton*

Several collections of *Oenothera* were made in the vicinity of the village of Houghton, which is on the shore of Portage Lake. Two disturbed areas, namely, the railroad tracks in town and the roadside south of town, gave rise to fine populations of *Oenothera*. These two localities were man-made and consequently weedy, but there is no reason to suppose that the evening primroses were other than those naturally occurring in the locality. Four distinguishably different types were found in these localities: 4438a (railroad tracks): calyx tips subterminal; inflorescence not declinate when young; bracts with definite abscission zone. (2) 4440 (railroad tracks): calyx tips terminal, in mature buds 5 to 7 mm. long; ovary not conspicuously red-papillate; stem conspicuously red-papillate. (3) 4233 (roadside): calyx tips terminal; ovary not conspicuously red-papillate, densely gray-pubescent. (4) 4235 (roadside): same type as Mandan 4431.

2. *Lake Linden*

This locality was a roadside about a half mile east of Lake Linden. The *Oenotherae* were growing in a broad, shallow depression between the road and a fence enclosing a cultivated field. The plants were tall and vigorous, and several fasciated specimens were found among them. Here the evening primroses were definitely more abundant because of recent movement and disturbance of surface soil and

probably represented the types originally found in or near the locality before the soil surface had been disturbed by the grading of the road. Eight collections were obtained at this locality, all belonging to the same type as Mandan 4431. They were 3662, 3663, 3664, 3665, 3665a, 3666, 3667, 3669.

3. *Dollar Bay*

This is a small village about four miles east of Hancock. A considerable amount of waste ground along the railroad tracks afforded an excellent disturbed habitat for the multiplication of *Oenotherae*. Five rather distinct types were collected here: (1) 3866, 3868, 3878: same as Mandan 4431. (2) 3883: calyx tips terminal; ovary conspicuously red-papillate; hypanthium yellow; stem, ovary, bud cone, and hypanthium only moderately pilose. (3) 3870: calyx tips terminal, those of mature buds 2 to 4 mm.; ovary not conspicuously red-papillate; stem not red-papillate. (4) 3874: calyx tips terminal; ovary not conspicuously red-papillate; bud cone with 8 stripes of purple splotches. (5) 3876: same as Houghton 4233.

4. *Otter Lake*

This lake, which is about fourteen miles south of the village of Houghton, has stretches of gravelly shore dominated by willow. Between the water and the road *Oenothera* was well established in several places. It is difficult in such a locality to appraise the effect of soil disturbance during road building, but one may say with fair assurance that, if there was any disturbance, the effect would have been to increase the abundance of the local types even if no others happened to be brought in. There proved to be four distinguishable types in the six collections made at this locality. They are: (1) 3818, 3832, 3861: same as Mandan 4431. (2) 3579: calyx tips terminal; ovary conspicuously red-papillate; hypanthium yellow; buds shorter than bracts; back of bracts, hypanthium, and bud cone with some red papillae. (3) 3861a: calyx tips terminal; ovary conspicuously red-papillate; hypanthium yellow; bracts shorter than buds; some red mottling and red-based papillate hairs on bud cone. (4) 3861b: calyx tips terminal; ovary conspicuously red-papillate; hypanthium yellow; stem, ovary, bud cone, and hypanthium conspicuously pilose; bracts densely pilose on white nerves below, with subglabrous, wine-red areas between veins.

5. *Jacobsville Quarry*

Jacobsville is on the east side of Portage Entry. At one time the quarrying of red sandstone was an important industry here, but the quarry has been abandoned for many years and the bottom is becoming overgrown with vegetation. In this new habitat *Oenothera* is one of the conspicuous pioneering genera, and two distinguishable types were collected in it. They are: 3597: same as Bete Gris Bay 3684, 3602: calyx tips subterminal; inflorescence declinate when young; ovary conspicuously red-papillate; hypanthium yellow; ridge at back of bract with red papillae extending onto it from stem ridge.

6. *Big Traverse Bay*

This is a broad bay on the east side of the Keweenaw Peninsula, lying between Traverse Point and the village of Gay. The gently sloping beach is almost pure sand with sparse vegetation. An unsurfaced road extends parallel to the beach, and along this road *Oenothera* was common. Here grading for the road has undoubtedly disturbed the soil enough to account for the large *Oenothera* population, but there is no reason to regard the types as other than native to the locality. Two distinguishable types were found: (1) 3660: same as Bete Gris Bay 3684. (2) 3661: same as Mandan 4431.

7. *Bear Lake*

This locality is about ten miles north of the town of Hancock and about one-fourth mile inland from Lake Superior. Two collections of *Oenothera* were made on the shore of the lake and were given the numbers 1231 and 3999. The former agrees with the type already described as Mandan 4431, and the latter is similar to Dollar Bay 3870.

8. *Silver Mountain*

This locality is in Laird Township. Most of the mountain has been burned, exposing large surfaces of bare granite with beautiful glacial striations. The plant cover on this surface is rather sparse, but *Oenothera* is one of the plants that have become established. The single type, No. 2298, agreed in its characteristics with Mandan 4431.

9. *St. Louis Hill*

This locality is about two miles east of the town of Laurium. A large population of *Oenothera* was found growing along an unsurfaced road. A sampling showed it to be uniform and the type to be distinct from that of any other locality. The two collections, 4354 and 4356, have the following distinguishing characters: calyx tips terminal; ovary conspicuously red-papillate; hypanthium with red flush; flowers small.

10. *Goose Neck Creek*

The Goose Neck Creek locality is about one mile northeast of Dollar Bay. A large colony of *Oenothera* was found on the open bank of the creek after it had emerged from a wooded gorge. The single type, which was collected under number 2687, has the following characters: calyx tips terminal; ovary conspicuously red-papillate; hypanthium yellow; buds shorter than bracts; stem, ovary, bud cone, and hypanthium conspicuously pilose; bracts without wine-red markings on back.

11. *Pilgrim River*

The Pilgrim River location is about two miles southeast of Houghton. The railroad right of way here provided a disturbed habitat favorable for a large population of evening primroses. The collections revealed two distinct types to be present: (1) 3595: same as West Bluff 1043. (2) 3595a: same as Phoenix Mine 2052.

12. *Canal Road*

This locality is about one mile west of the village of Houghton near the present site of the Bosch Brewery. An *Oenothera* population occurred between the road and the railroad on a strip of land largely overgrown with weeds. A single collection, number 2241, proved to be a distinct type. Its distinguishing features are: calyx tips subterminal; inflorescence not declinate when young; bracts lacking a definite abscission zone; ovary conspicuously red-papillate.

BARAGA COUNTY

1. *Baraga*

This locality presented an artificial habitat on which *Oenothera* maintains a large population very successfully. It is an open stretch

of land along railroad tracks north of the town of Baraga. Here the surface disturbance so conducive to a large *Oenothera* population was caused by grading when the railroad was constructed. A sampling of the population revealed three distinguishable types, all of which have been found elsewhere: (1) 4315: same as Phoenix Mine 2052. (2) 4337: same as West Bluff 1043. (3) 4338, 4341: same as Mandan 4431.

2. *Pequaming*

This locality is not in the Keweenaw Peninsula, but is included in order to provide a comparison with the population found on the opposite shore of Keweenaw Bay at just the same distance from the head of the bay. Pequaming is an abandoned lumbering town about eight miles north of L'Anse. It is dominated by a large sawmill no longer in operation. At the eastern edge of town there is a rather extensive open area largely covered with sawdust and overgrown with weedy plants. *Oenotherae* were conspicuous among them. A sampling of the large population gave four distinguishable types, as follows: (1) 4253: same as Dollar Bay 3883. (2) 4254: same as West Bluff 1043. (3) 4262, 4294, 4296, 4303: calyx tips subterminal, 2 to 3 mm. long; inflorescence not declinate when young; bracts without definite abscission layer; ovary not conspicuously red-papillate, not densely gray-pubescent. (4) 2041, 4253, 4261, 4262, 4287, 4290, 4293, 4304: same as Mandan 4431.

At the twenty-two localities described twenty-one different types were discovered which appear to have a genetic basis and to warrant systematic recognition in a critical flora. A more thorough collection in the area would certainly reveal additional types that are not accounted for here, and it is hoped that in the future more extensive work will be done in order to discover other entities.

I think it might be helpful to future workers in the area to have a summary of the foregoing data in the form of a key constructed for the twenty-one types that were distinguished. I am especially indebted to Professor H. H. Bartlett, of the University of Michigan, for valuable assistance in the preparation of this key:

A. Calyx tips terminal

B. Ovary conspicuously red-papillate

C. Hypanthium with red flush; flowers small (St. Louis Hill 4354, 4356)

- C. Hypanthium not reddish; flowers medium
 - D. Buds shorter than bracts
 - E. Back of bracts, hypanthium, and bud cone with some red papillae (Otter Lake 3579)
 - E. Back of bracts, hypanthium, and bud cone without red papillae
 - F. Stem, ovary, bud cone, and hypanthium conspicuously pilose
 - G. Bracts densely pilose on white nerves below, with subglabrous, wine-red areas between veins (Otter Lake 3861b)
 - G. Bracts without subglabrous, wine-red marking on back (Goose Neck Creek 2687)
 - F. Stem, ovary, bud cone, and hypanthium only moderately pilose (Dollar Bay 3883; Pequaming 4253)
 - D. Bracts shorter than the buds
 - H. Some red mottling and red-based papillate hairs on bud cone (Otter Lake 3861a)
 - H. Bud cone not red-mottled nor red-papillate (Mandan 4431; Fort Wilkins 2522; Lake Upson 3797; Houghton 4235; Lake Linden 3662, 3663, 3664, 3665, 3665a, 3666, 3667, 3669; Dollar Bay 3866, 3868, 3878; Otter Lake 3818, 3832, 3861a; Big Traverse Bay 3661; Bear Lake 1231; Silver Mountain 2298, 2620; Baraga 4338, 4341; Pequaming 2401, 4253, 4261, 4262, 4287, 4290, 4293, 4304)
- B. Ovary not conspicuously red-papillate
 - I. Ovary densely gray-pubescent (Dollar Bay 3876; Houghton 4233)
 - I. Ovary not densely gray-pubescent
 - J. Bud cone with 8 stripes of purple splotches (Dollar Bay 3874)
 - J. Bud cone without 8 stripes of purple splotches
 - K. Calyx tips of mature buds 5 to 7 mm. long; stem conspicuously red-papillate (Houghton 4440)
 - K. Calyx tips of mature buds 2 to 4 mm. long; stem not red-papillate (Dollar Bay 3870; Bear Lake 3999)
- A. Calyx tips subterminal
 - L. Inflorescence declinate when young
 - M. Ovary conspicuously red-papillate, especially toward apex
 - N. Hypanthium red (Great Sand Bay 2770, 3806)
 - N. Hypanthium not red
 - O. Ridge at back of bract with red papillae extending onto it from stem ridge (Jacobsville 3602)
 - O. Ridge at back of bract without red papillae (Bete Gris Bay 3684; Jacobsville 3597; Big Traverse Bay 3660)
 - M. Ovary not conspicuously red-papillate
 - P. Hypanthium red (Eagle River 4832)
 - P. Hypanthium not red
 - Q. Ovary very densely and hypanthium densely viscid-pubescent, both pilose but with no visible crispate short pubescence among the pili (West Bluff 1043, 2443, 3789; Baraga 4337; Pilgrim River 3595; Pequaming 4254)
 - Q. Ovary almost lacking viscid pubescence, but with dense crispate

pubescence among the pili. Hypanthium only moderately viscid pubescent (Phoenix Mine 2052; Baraga 4315; Pilgrim River 3595a)

L. Inflorescence not declinate when young

R. Bracts with definite abscission zone (Houghton 4438a)

R. Bracts without definite abscission zone

S. Ovary conspicuously red-papillate (Canal Road 2241)

S. Ovary not conspicuously red-papillate

T. Calyx tips 0.5 to 1.0 mm. long; ovary densely gray-pubescent (Eagle River 4375)

T. Calyx tips 2 to 3 mm. long; ovary not densely gray-pubescent (Pequaming 4262, 4294, 4296, 4303)

Other arrangements of the distinct entities would have been equally logical. It must be remembered that in *Oenothera* very widely different and true-breeding types may have exactly the same parentage. New types may come into existence by mutation as well as by hybridization, and such types may carry their distinctive genes in one of two complementary gametes, which sometimes function only as eggs, or only as sperms. Entities which appear to be very similar may actually have less in common, genetically, than others which seem widely unlike.

Under these circumstances it is more or less by arbitrary choice that one makes key distinctions. Others might be equally logical. From the standpoint of practical systematics it is best to avoid dependence upon features of growth habit and branching, which herbarium specimens of such large coarse plants can seldom show, but, rather, to rely upon the more minute distinctions which may be apparent in any herbarium specimen collected at flowering time. So far as there is evidence, many true-breeding and distinctive *Oenotherae* are extremely local. How many of them it may be practicable to distinguish does not yet appear, and only further studies such as the present one will indicate it. An effort to apply similar criteria at other localities may suggest what types or groups of types are most wide-ranging, and, therefore, from the standpoint of practical floristics, are most worthy of naming.

BERMUDIAN MARINE VAUCHERIAS OF THE SECTION PILOBOLOIDEAE*

WM. RANDOLPH TAYLOR AND ALBERT J. BERNATOWICZ

WHEN, during the spring of 1949, the writers undertook their studies of the marine algal vegetation of Bermuda, it was recognized that quite unexpected little problems might arise to deflect attention from the primary objects in view, and might well prove of considerable worth. This has certainly been true of a search started near the aquarium at the village of Flatts, directed toward finding good material of the marine *Dichotomosiphon*, which Collins and Hervey (1917) had reported from the inlet to Harrington Sound immediately adjacent to the aquarium grounds. The vaucheriacious plant which was particularly observed formed abundant aplanosporangia, but unlike those of *Dichotomosiphon*, and obviously of a diffuse species unknown at Bermuda. A similar plant has been reported from Connecticut, but was known to the authors only by repute (Taylor, 1937, p. 101). Sexual reproduction was only belatedly and sparsely found in preserved material. Consequently, in the winter period of 1950-51 the junior author made special efforts to locate this delicate *Vaucheria* at the original and many other localities, and was successful at several of them. Cultures were established, and it then became apparent that not one but two species were involved, both in the same section of the genus. One, *Vaucheria piloboloides* Thuret (1854), we shall describe and illustrate from our preserved material, since no such detailed observations have ever been reported from American material. The other species, which we propose to name *Vaucheria bermudensis*, was thoroughly studied both from preserved material and from plants brought to Michigan alive and fertile. It differs in many details, as will shortly appear.

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In Bermuda these two *Pilobolus*-like species of *Vaucheria* are common inhabitants of sandy bottoms in quiet waters. In areas containing much black decaying organic matter, as at Coopers Island, the sand is soft and suggestive of gritty mud. Here they form fine, diffuse patches one to two centimeters high and several square meters in extent; they climb over the occasional stones, which they tend to bury by the accumulation of sand among the filaments. In cleaner situations, as at a small unnamed cove on the north side of Smiths Island, the bottom is firmer, and the colonies (in this case *V. piloboloides*) bind the sand to form hemispherical domes 1.5–2.0 dm. in diameter, but the filaments clear of the sand are not longer than those on softer substrata. The upper portions of the colonies in either habitat are laid bare at low tide, whereupon they lie flat as a green film, but the capillarity of the sand never permits the exposed portions to become dry. At low tide no part of the colony is more than two decimeters below water, and at the lowest tides all or practically all the growth is exposed. These plants are common and widespread at Bermuda throughout at least the first half of the year. While they can be distinguished with tolerable ease from other *Vaucheriae* known to occur in the area, they cannot be distinguished from one another except in the presence of the sexual fruiting structures.

Fruiting material was difficult to recognize in the field because obscured by grains of sand, which were unavoidably lifted with the specimens to be examined. Furthermore, freshly collected material was rather scantily in fruit at this season. However, when kept in white enameled trays on outdoor aquarium tables and continuously but gently bathed by running sea water for from several days to three weeks, the plants fruited abundantly, the numerous fertile tips being silhouetted against the white trays and appearing as dark-green areas capping the vegetative growth.

The Bermudian plants of *Vaucheria piloboloides*¹ resemble the

¹ Stations for *V. piloboloides* Thur., which were confirmed by material with mature oöspores include: Wells Bay, Coopers I., no. 50–427, 8 Dec. 1950; cove on the north side of Smiths I., no. 51–839, 2 Feb. 1951; near the Bermuda Biological Station, St. Georges I., no. 51–626, 8 Jan. 1951.

European type rather closely. The irregularly branching filaments, 26–66 μ in diameter, bear the reproductive organs near the tips. In general, one antheridium and an oogonium appear close together, the latter overtopping the former. The antheridium seems always to be initiated first, but it does not necessarily discharge its antherozoids before the oöspore has appeared and matured (compare Pl. I, Figs. 1, 2 with 5, 6). Between the antheridium and the green vegetative filament there is cut off a cell which does not become inflated, but which retains the diameter of the filament or even collapses a little. It soon becomes empty and colorless. In length it is usually nearly twice the diameter, occasionally to more than three times. The antheridium is at first cylindric-lanceolate to spindle-shaped (Pl. I, Figs. 6, 7), but with maturity generally becomes stouter, a little inflated, and irregular because of the development of the lateral discharge pores, which are generally prominent or even tubular, and single (Pl. I, Figs. 4, 8, 9), sometimes two (Pl. I, Fig. 2), sometimes obscure (Pl. I, Fig. 1). Rather frequently, but not uniformly, a pore opens at the apex as well. The length ranges from 160 μ to 200 μ ; the diameter, exclusive of the pore tubes, from 30 μ to 45 μ .

The oogonial branchlets always arise close below the antheridial supporting cells. They grow as erect clavate structures, which enlarge rapidly and become sharply inflated at the summit (Pl. I, Figs. 1–4). A cross wall is then formed a short distance up the stalk portion, and the withdrawal of the cytoplasm toward the distal end follows. The fertilization pore is obscure but probably terminal. The fertilized egg develops a compact form at the distal end of the oogonium and, after fertilization, a firm but not very thick oöspore wall; it is securely anchored to the wall of the oogonium by a zone of attachment perceptibly below the end of the spore. The diameter of the lowermost stalk portion of the oogonium after spore maturation is that of the filament, but increases somewhat upwardly for about one half to two thirds of the total length, where the oogonium is sharply inflated to form the nearly spherical summit. There is rather frequently a sharp ring about the stalk near the inflation (Pl. I, Figs. 5–7), apparently a thickening of the wall, but no septum has been seen to accompany this ring. The length of the mature oogonium ranges from 320 μ to 500 μ , the diameter from 140 μ to 210 μ , averaging 380 $\mu \times 161 \mu$. The oöspores are peculiar, not only in giving the characteristic *Pilobolus*-like aspect to the oogonia, but in being somewhat compressed (Pl. I, Figs. 10–14). Spores for meas-

urement must be carefully selected because they tend to be pushed out of alignment by any pressure on the oögonia. From several measurements we secure a range in length of $75\ \mu$ to $110\ \mu$; in transverse diameter, of $105\ \mu$ to $145\ \mu$. The mean length is $85.7\ \mu$, and the standard deviation is $8.4\ \mu$. The mean diameter is $119.3\ \mu$, and the standard deviation is $12.4\ \mu$. The ratio of spore length to spore diameter averages 1:1.39. Correspondingly, the ratio of spore diameter to oögonium diameter averages 1:1.35.

Unfortunately the available European citations of this species are very niggardly in data. The brief original description (Thuret, 1854, p. 389) carried no illustration; the localities given are on the Channel coast of France. Kützing (1856, p. 20, pl. 55, fig. 1) described a similar plant from near Brest as *V. fuscescens*. Walz (1866) in his monographic paper does not figure the species, but puts *V. fuscescens* in synonymy. Though our plants showed less elaborately branching clusters of fruit than did those figured by Woronin (1869, pl. 2) from the Mediterranean coast of France, they agree well in other respects. Le Jolis (1864) quotes Thuret at some length to amplify and add to the original description, but figures only the aplanosporangium and, imperfectly, the oögonium, being on the whole less informative than Woronin. Ernst (1904) gives excellent figures of aplanosporangium formation and germination at Naples, but does not discuss the sexual reproduction, whereas Migula (1907, p. 874) ascribes the plant to the Adriatic, these two stations suggesting warm-water affinities. Heering (1921), however, records it from Warnemünde² on the western Baltic coast of Germany. Doubtless there are other European records, but the species apparently is not abundant enough to have been very critically studied and measured, since Hamel (1931, p. 428, figs. 33, II, 33, III) copies Woronin's old figures, and Dangeard (1939) furnishes neither new figures nor data.

So far as the American record² is concerned, it is based on Collins' specimen no. 476 in the Phycotheca (1898), which the senior author attempted to study microscopically, but failed to revive sufficiently. Collins' variety *compacta*, published as no. 477 in the same collection,

² After this paper had been submitted for publication Cand. mag. Tyge Christensen (København), who has studied the genus extensively, kindly informed us that the Warnemünde record was based on Hauck et Richter: *Phyk. Univ.* no. 282, but that the material had been misidentified. It consists of a dioecious species, apparently the one which Collins similarly confused with *V. piloboloides* in *Phyc. Bor. Am.*, the correct name for both being *V. compacta* (Coll.) Coll.

he later came to consider a distinct species, but the original collection likewise proved obdurate. Brown (1929), monographing the American members of the family, seems to have had nothing to add from personal observations on these particular species. She includes "Asiatic Sea" in the list of localities, but this is probably an erroneous substitution for Adriatic Sea, rather than a range extension.

In our investigation it soon became evident that there are two entities in the Bermudian material, the second of which, unless oöspores are present, cannot be distinguished from *V. piloboloides*. When the spores are present, their size relative to the oögonia and their proportions make them readily distinguishable. With one possible exception, there is no other species with characters which come at all close, since the habit of growth, spherical spores, and scattering of the sex organs seem to rule out *V. compacta*. The possible exception is *V. longicaulis* Hoppaugh (1930) from mud flats in Monterey County, California. Dr. Hoppaugh, however, definitely states that in *V. longicaulis* the oöspores are subspherical, which they clearly are not in *V. bermudensis*, and she figures them as free from the oögonial wall, which they are not at any stage short of final release in either *V. piloboloides* or *V. bermudensis*. In respect to the antheridia, she states that the usual number of projecting pores is five to eight, whereas in our plant it is usually one or two, and very rarely more.³ It would have been much more satisfactory if Dr. Hoppaugh had given a good series of measurements of mature spores, but she expresses distrust of such data, basing her position on uncertainty regarding maturity. We found no difficulty in regard to spore maturity, for the light-brown spore wall was thick enough to be distinctive in both species. The spore sizes also held close to the average for the species. The variation in oögonial size appeared to us to be considerable, contrary to her findings in *V. longicaulis*, although the general shape was in most cases distinctive.

The colonies of *V. bermudensis* are diffuse and appear as very light green clouds of filaments, through which the sand below readily appears. The lower, older, filaments ramify among the grains of sand. They are frequently septate (Pl. II, Fig. 2), but the younger filaments are not (Pl. II, Fig. 1). Rather frequently sharp inflations

³ In one specimen, without oögonia, occurring in a unique stagnant salt-water pond on Paget Island, antheridia bore several discharge pores, but it was not possible to establish any connection with identifiable material of this or any other species.

of the main filament axes or of side branches occur without distinctive contents, but these are considered abnormalities (Pl. II, Fig. 5). Among the filaments near the substratum one sometimes finds those in which a very deep green color is particularly evident and which are inflated at the ends, sometimes simply (Pl. II, Fig. 3), sometimes digitately (Pl. II, Fig. 4), sometimes with much longer branches. These have very dense cytoplasm and reduced vacuoles, yet may show cyclosis. It may be suggested that they are some sort of perennating organ, but, since no wall segregates them, one can hardly consider them equivalent to akinetes. Certainly they are not malformations due to injury.

As fruiting time approaches, the tips of the rather simple young erect branches become clavate, and the terminal spores are cut off by transverse walls (Pl. II, Figs. 6-9). A few empty sporangia were seen, and a few germinating spores, which almost certainly were aplanospores, but the process was not studied in detail. The aplanosporangia were observed to germinate and form a filament from the tip without first being discharged, but this was rare. The axis could grow forward from below an aplanosporangium to form a new actively growing tip.

The antheridia appear in a culture somewhat later than the aplanosporangia and independent of them. Both the terminal fertile cell and the supporting cell below it are at first green, but the latter soon appears empty. Its lateral walls seem thin and tend to collapse readily, so that the end walls often curve into it because of the turgor of the adjoining green parts. This cell is seldom shorter than its breadth, but equally seldom it is more than twice as long (Pl. II, Fig. 11), the dimensions being $18\ \mu$ to $50\ \mu$ in diameter and $25\ \mu$ to $65\ \mu$ in length, with the average about $34\ \mu \times 42\ \mu$. Typical cases appear in Plate II, Figures 12-17. The rare exceptions were especially studied, and consequently the figured examples are rather numerous. A plant in which the antheridium is subtended by a single wall, yet apparently functioned normally, shows in Plate II, Figure 12, and another with a very oblique wall in Plate III, Figure 3. These were less common than cases in which three walls and hence two supporting cells appear (Pl. III, Figs. 2, 5, 6), of which the lower commonly retains a little chlorophyll.

Early in the period of sexual activity, and particularly in some examples, only antheridia occur. Under such circumstances they

are especially liable to follow one another in succession, an erect outgrowth from below the first antheridium developing a second antheridium a bit higher, succeeded by another in turn (Pl. II, Figs. 10, 12). It was otherwise rare to find a second antheridium developed before an oögonium appeared. Such male plants could not be identified with certainty, but it cannot be assumed that they represent a dioecious species. More probably they are simply cases of delayed development.

Since the senior author saw only incompletely developed plants in the field and since his junior colleague was too preoccupied with other tasks to give sufficient time to it, details of cell division in the development of antheridia and antherozoids were not followed. The antheridia are at first nearly cylindrical (Pl. II, Figs. 10-12), later more nearly spindle-shaped, very often with the distal end somewhat extended and curved to one side (Pl. II, Figs. 13, 14). The subtruncate tip commonly, but by no means always, acts as a discharge tube (compare Pl. III, Figs. 2, 4, 5 with Figs. 3, 6, 7). There is practically always at least one lateral discharge pore (Pl. II, Figs. 14, 15; Pl. III, Figs. 2, 3, 5, 7) and perhaps more usually two (Pl. II, Figs. 16, 17; Pl. III, Figs. 4, 6). The formation of abortive pores (Pl. II, Fig. 13) was not often noted. In only one collection, entirely without oögonia and so not to be identified, did we find very elongate multipored antheridia. Discharge pores are nearly always elevated, sometimes into short (Pl. III, Fig. 2), sometimes into longer (Pl. II, Fig. 15; Pl. III, Figs. 4, 7) tubular projections, but the average lies somewhat between.

The dimensions of the antheridia vary a good deal, and more so in the absence of oögonia. The figures from identifiable samples show a range in diameter (excluding discharge tubes) of $26\ \mu$ to $50\ \mu$; in length, from $219\ \mu$ to $464\ \mu$, with averages about $38\ \mu \times 331\ \mu$.

Oögonia were formed abundantly in two samples. The senior author was able to study preserved material of these, and of living specimens brought back in February, 1951, and to confirm and extend the observations made in the field by the junior author. Oögonia were not observed except in succession after the appearance of antheridia. The formation of two pairs of organs on a filament was not common. The antheridium sometimes matures before the oögonial branch is well developed, even to the point of discharge; sometimes it delays and the oöspore matures while the antheridium

still has no discharge pores. The outgrowth of the filament comes from below the antheridial supporting cell (Pl. III, Fig. 1), sometimes close, sometimes far down the filament, turns sharply upward, far exceeding the antheridium, and is cut off by a wall at about the mid-height of this structure (Pl. III, Figs. 4, 5). Rarely one of the ordinary filament cross walls appears in the oögonial branch (Pl. III, Fig. 7) or below the antheridium (Pl. III, Fig. 2). The cytoplasm in the oögonium then contracts, maintaining its contact very tenaciously with the distal end wall of the oögonium, leaving behind an essentially protoplasm-free space. Rather often a line, usually a little irregular, is visible on the oögonial wall about halfway up (Pl. III, Figs. 5, 7, 11). In a few plants the protoplasm could be clearly seen to pass this line and demonstrate the absence of a septum. In others there was reasonable assurance that a septum was present, and yet the lower cell thus formed contained little protoplasm, and so was probably segregated after the bulk of the cytoplasm had retracted toward the tip. This condition may represent the last trace of a tendency to form an oögonial supporting cell.

Most of the oögonia seen were either rather young or with mature oöspores. In the living as well as in the preserved material some examples did show what may be interpreted as the receptive stage for fertilization. The oögonial protoplasm then lies strictly at the end of the oögonium. No clear wall could be detected across the tip, but a little to the side the wall appears, closely encircling the cytoplasm, which even seems to project just a little. The oögonial protoplasm shows little suggestion of a central vacuole at the time, and has a fairly well defined lower border, with the chromatophores generally disposed except at the small area closely encircled by the wall, which is the clear gray of alveolate cytoplasm and may be the receptive region.

When the oöspores are mature, the oögonial wall continues to adhere. Consequently, whatever exists beyond the equator of the spore seems a part of the spore wall. Among great numbers studied no spore was seen loose in its oögonium (though pressure deformations of the oögonium may give such a first impression falsely), and no instance of spore discharge was observed.

The shape of the oögonium must be contrasted with that of *V. piloboloides*. The stalk portion of the oögonium of *V. bermudensis* enlarges somewhat more considerably, but at about three fifths of

the distance from the base it ceases to swell and extends up to the equator of the spore without much further increase. Sometimes this is markedly a sharp change in contour (Pl. III, Figs. 4, 6, 7), generally it is less sharp (Pl. III, Figs. 9, 10), but a little loss of turgidity or displacement in mounting will conceal this feature, which is otherwise evident to the critical eye. The oögonium so produced is distinctive in shape and is much less inflated than that in *V. piloboloides*. Though the typical shape of the oögonium in *V. piloboloides* is in the fullest expression nearly spherical on a cylindrical stalk, in *V. bermudensis* it may be better described as turbinate. The oögonial wall of the inner tapered portion is thin and smooth; that of the outer portion near the spore can be seen under intense illumination through a very small diaphragm aperture to be a little thicker (or more refractive) and to be obscurely, irregularly, and rather coarsely rugose. The dimensions of the oögonia range in diameter of the outer end from $116\ \mu$ to $153\ \mu$, and in length from $285\ \mu$ to $510\ \mu$, the average being about $131\ \mu$ by $388\ \mu$.

The oöspores are depressed-spherical to transversely elliptical (Pl. III, Figs. 6-13), with a brown apparently simple smooth wall about $2\ \mu$ thick, although a very few with a clear refractive wall $4\ \mu$ thick were seen. Usually the portion beyond the equator or zone of greatest diameter is about hemispherical. Unless the spore is viewed strictly from the side, this is not evident. The diameter of the oöspores ranges from $105\ \mu$ to $141\ \mu$, with the mean about $120\ \mu$ and the standard deviation $8.4\ \mu$. The oöspore length has a range from $90\ \mu$ to $136\ \mu$, and its mean is at $105\ \mu$, with the standard deviation $8.5\ \mu$. The ratio of spore diameter to oögonium diameter averages 1:1.08 (compare with the ratio of 1:1.35 in *V. piloboloides*). The ratio of spore length to spore diameter averages 1:1.15. To compare this ratio with the oöspore proportions of *V. piloboloides*, 1:1.39, we have calculated the statistic t and found it to be 11.6 (degrees of freedom = 61) (Snedecor, 1946). The probability of getting such a large value of t is less than one in one thousand, if we assume that only one population furnished both groups of collections (Fisher and Yates, 1949). The indication is strong, therefore, that the two groups of samples which furnished the oöspore ratios represent two distinct populations.

We therefore offer a technical description of this new plant as: *Vaucheria bermudensis* sp. nov.—Tabb. II-III.—Plantae colonias dif-

fusas formantes; filamenta 18–51 μ diam., irregulariter patenterque ramosa; rami sporangiales clavati; aplanosporangia clavata ad obovata, 80–110 μ diam., 212–240 μ long. Antheridia primum in ramo terminalia, in cellula vacua sustinente portata, subcylindrica ad subfusiformia, 26–50 μ diam., 219–464 μ long., 1–2 poris lateralibus praedita. Oögonia turbinata ad clavata, stipitata, e situ infra antheridia singulatim orientia necnon haec superantia, a filamentis per septum sejuncta, 285–510 μ long., 116–153 μ diam., prope fastigium paululum expansa. Oosporae in latere inferiore subcompressae, 105–141 μ diam., 90–136 μ long. Specimen typicum in loco dicto Shore Hills, St. Georges I., Bermuda, legit A. J. Bernatowicz no. 51–790, 27 Jan. 1951.

Vaucheria bermudensis sp. nov.—Plates II–III.—Plants forming diffuse colonies; filaments 18–51 μ diam., irregularly and patently branching; sporangial branches clavate; aplanosporangia clavate to obovoid, 80–110 μ diam., 212–240 μ long. Antheridia at first terminal on a branch, borne on an empty supporting cell, subcylindrical to subfusiform, 26–50 μ diam., 219–464 μ long, with 1–2 lateral pores. Oögonia turbinate to clavate, stalked, arising singly from below the antheridia and overtopping them, separated by a cross wall from the filament, 285–510 μ long, 116–153 μ diam., slightly expanded near the tip. Oöspores generally somewhat compressed on the lower side, 105–141 μ diam., 90–136 μ long. Type specimen from the well of the tide gauge at the Bermuda Biological Station, Shore Hills, St. Georges I., Bermuda, collected by A. J. Bernatowicz no. 51–790, 27 Jan. 1951.

Additional stations for *V. bermudensis* which were confirmed by material with mature oöspores include: Flatts, near the government aquarium, on Hamilton I., no. 49–173, 9 March 1949 and no. 49–880, 22 April 1949; Vaughans Bay (also called Whites Bay) on the east end of St. Davids I., no. 51–718, 20 Jan. 1951.

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EXPLANATION OF PLATE I

Vaucheria piloboloides

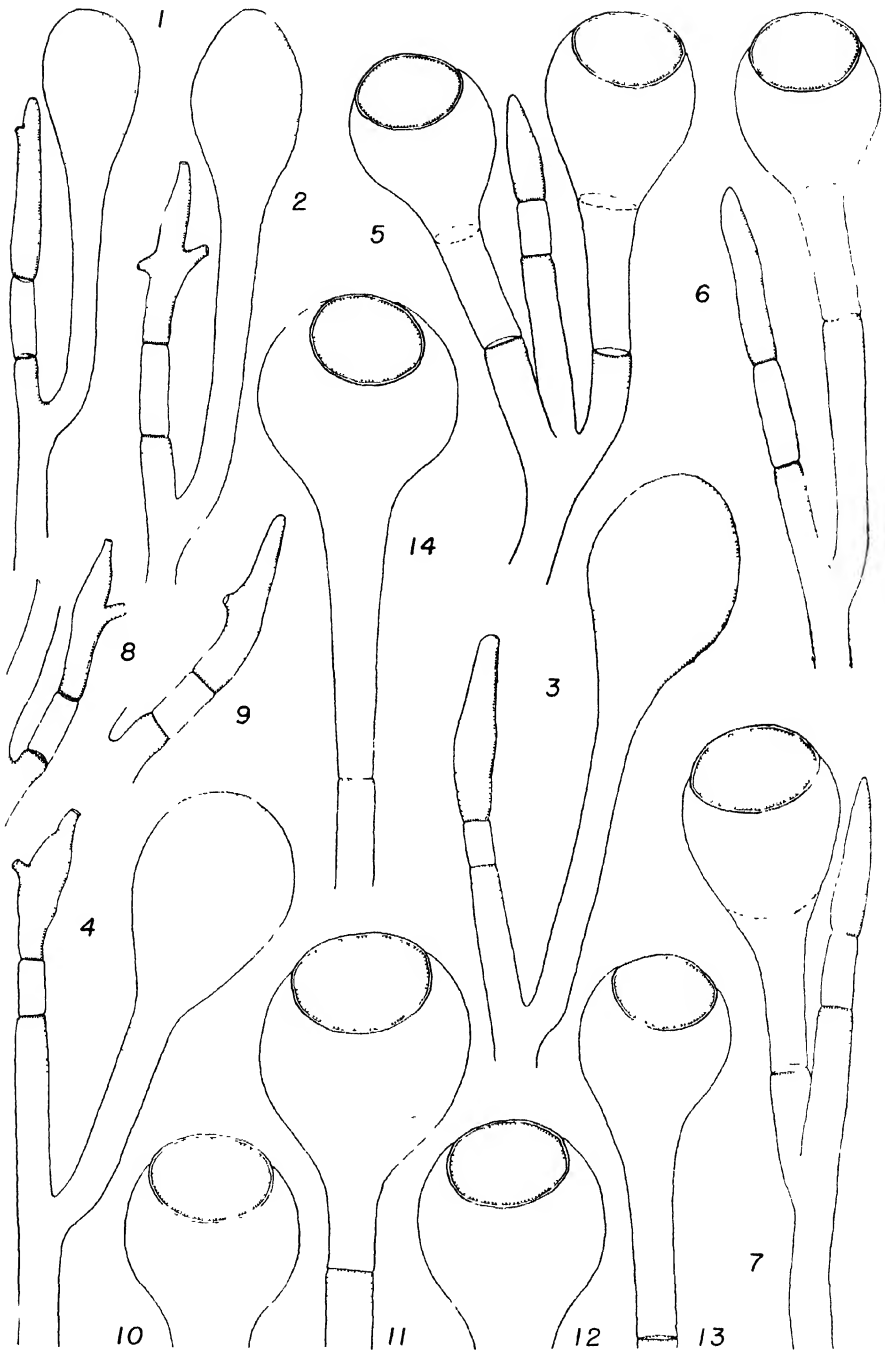
(All figures $\times 140$)

FIGS. 1-4. Branchlet tips with young oögonia. The antheridium in Figure 3 has not yet developed discharge pores, but those in the other figures have matured

FIGS. 5-7. Branchlet tips with mature oöspores in the oögonia; here also the antheridia are young

FIGS. 8-9. Individual mature antheridia

FIGS. 10-14. Individual mature oögonia with oöspores



Vaucheria piloboloides

EXPLANATION OF PLATE II

Vaucheria bermudensis

(All figures $\times 100$ except as marked)

FIG. 1. A young portion of a branch system (a short section omitted to save space) showing alternate branching.

FIG. 2. An old portion of such a system, showing cross walls.

FIGS. 3-4. Tips of lower branches with congested contents. $\times 140$

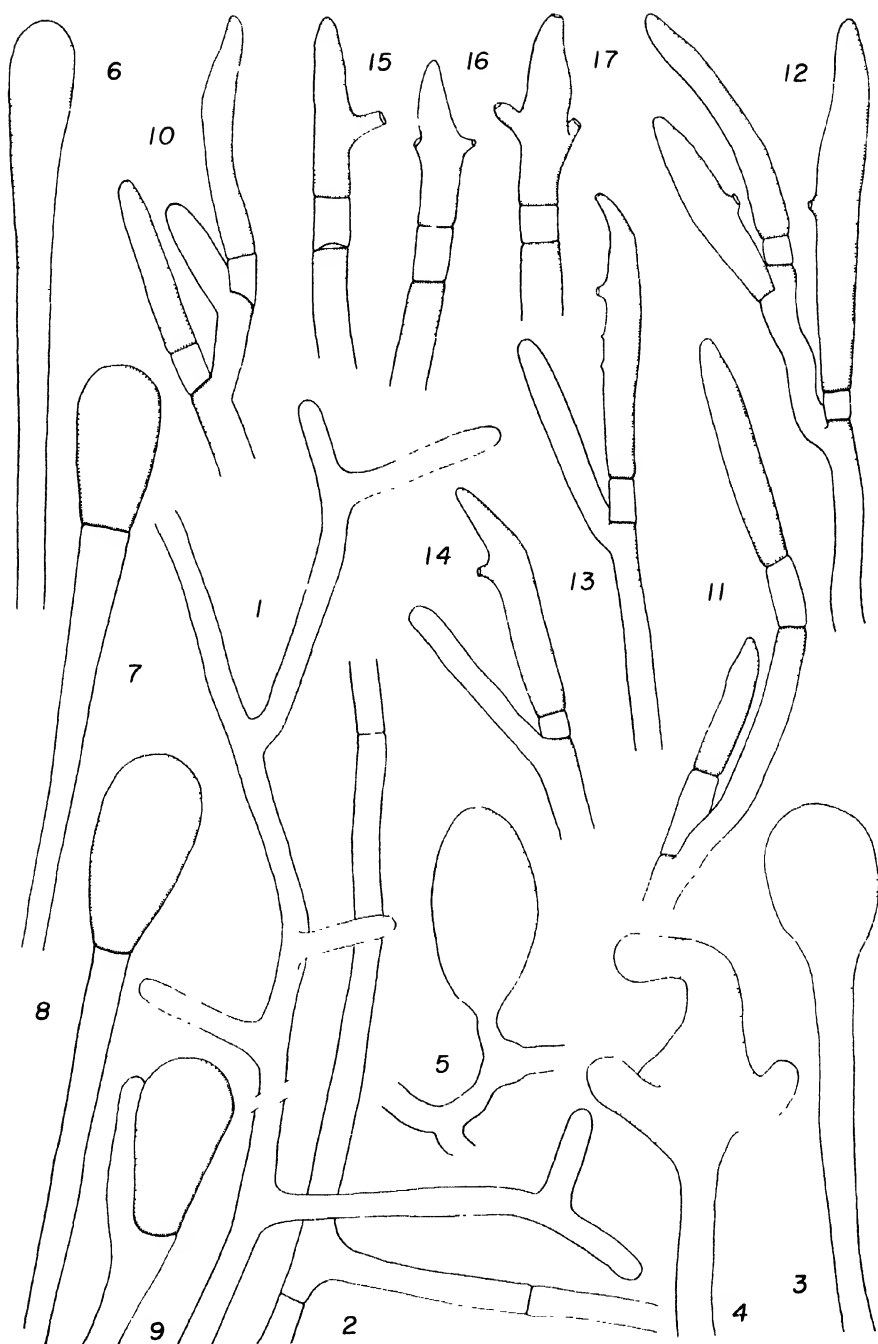
FIG. 5. A short vesicular lateral branchlet, considered an abnormality.

FIGS. 6-9. Stages in the development of aplanosporangia from erect branch tips.

FIGS. 10-11. Young branch tips showing development of successive young antheridia.

FIGS. 12-14. Similar tips with mature antheridia.

FIGS. 15-17. Mature antheridia as associated with oogonia. $\times 140$



Vaucheria bermudensis

EXPLANATION OF PLATE III

Vaucheria bermudensis

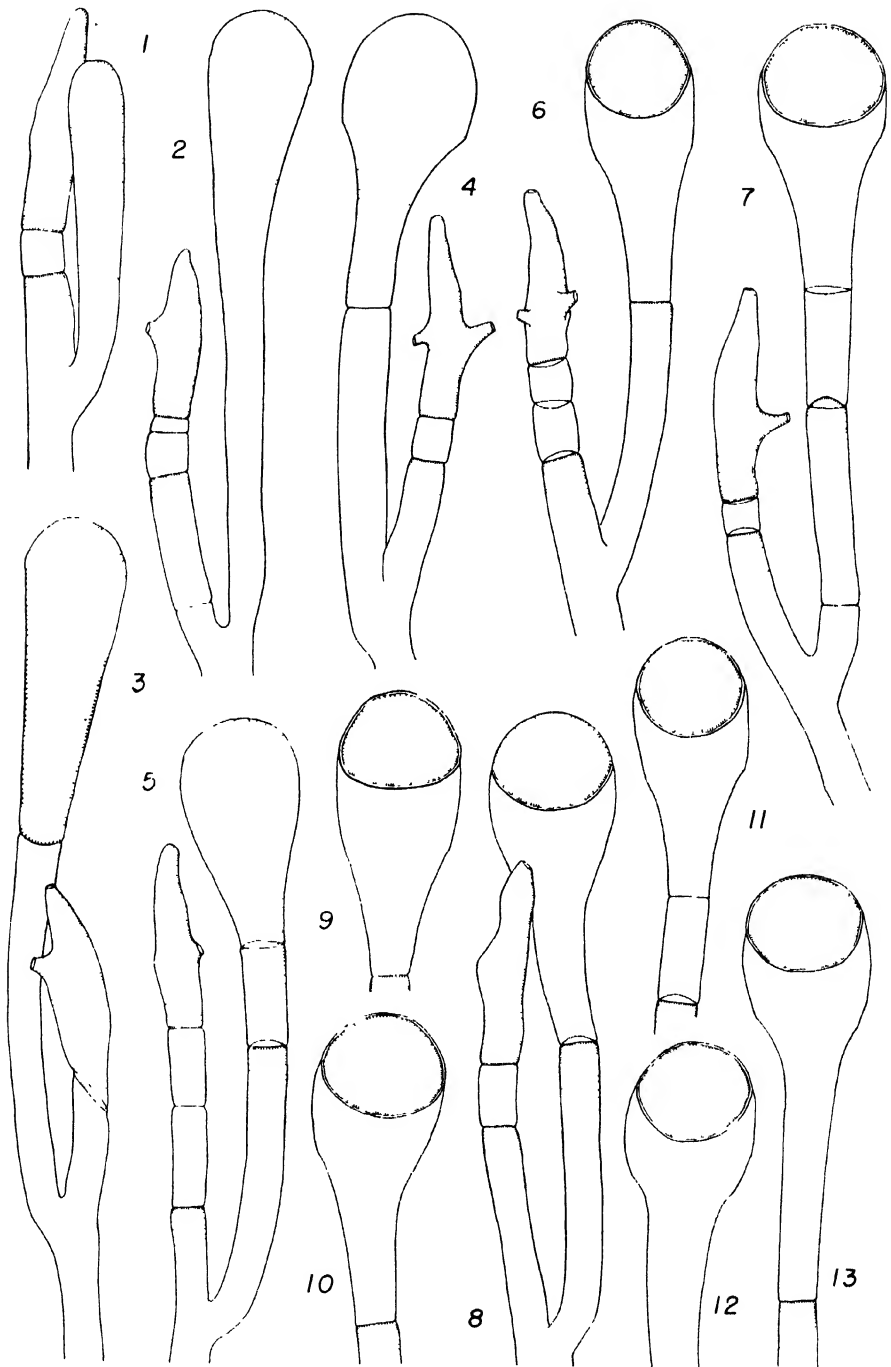
(All figures $\times 140$)

Figs. 1-2 Young stages in the development of an oogonial branchlet

Figs. 3-5 Somewhat later stages, with the segregation of the oogonium completed

Figs. 6-8 Branchlets with mature antheridia and mature oospores

Figs. 9-13 Mature oospores in their oogonia



Vaucheria bermudensis

CYSTOPTERIS BULBIFERA (L.) BERNH., A CONVENIENT SOURCE OF APICAL CELLS FOR SLIDES

KATHARINE TRYON

BOTANISTS who teach classes in morphology and who are interested in the apical cell of the Pteridophytes usually find it difficult to demonstrate this phenomenon in stems. Two things primarily contribute to the problem. First, the growing apex of a rhizome is almost impossible to find in many temperate-zone ferns, and, second, the apical cell is likely to lie in a considerable mass of tissue. These difficulties are usually circumvented by using the root, which is smaller and in which the apical cell can be quite easily found in sections. Even when roots are used, the fern must still be dug up. The method suggested in this paper involves remarkably little effort beyond locating a stand of the fern.

Cystopteris bulbifera (L.) Bernh. is a cosmopolitan species. Specimens collected from many areas in the eastern and central United States are included in the University of Michigan Herbarium, and among them are examples from seventeen different locations in Michigan alone, representing a range covering nearly the entire state. The plant appears to grow in more or less isolated communities or clumps. It has been collected by the writer in Reese's Bog on the west shore of Burt Lake in Cheboygan County, Michigan, where it tends to grow in open areas on the otherwise densely shaded bog floor. It has been most frequently collected by others along stream banks in the shade, and on shady limestone cliffs. Generally speaking, the fern grows well in a variety of habitats.

C. bulbifera is easily recognized by the elongated older fronds with many fleshy-scaled buds, or bulbils, attached to the lower surfaces (Pl. I, Figs. 1-2). The bulbils average from four to five millimeters in diameter when fully developed.¹ Size seems to bear no relation to maturity, for small ones grow into new plants as readily

¹ Matouschek (1894) and Rostowzew (1894) have both described these bulbils in detail.

as do large ones. Fully developed bulbils of all sizes are present on the fronds as early in the season as late June. They fall off very easily, and many germinate at once, producing new sporophytes in the same season that they themselves are formed. These adventitious buds apparently constitute the only means of reproduction of the fern, since the writer's own and all other reported attempts to germinate the spores in the laboratory have failed.

When dissected and examined, the bulbil of *C. bulbifera* is found to consist of from two to five fleshy scales attached at the base to a very small tomentose "axis." If the buds are placed in damp chambers on moist paper, or in wet sphagnum, roots develop perceptibly from the basal end within four or five days. These roots are followed by the appearance of a young leaf at the apex. Usually just one leaf is first formed by a single bulbil, and it will reach a length of several centimeters before another appears. Because of the abundance of stored starch in the fleshy scales, these young plants will grow for at least six months on moist paper alone. In petri dishes they are easily maintained, since they are not readily subject to attack by fungi. In sphagnum in the greenhouse new sporophytes can be grown to considerable size, and a crop of bulbils can be harvested from them in five months or less. The writer has kept two six-inch pots of the fern for nearly 20 years, collecting bulbils at intervals. Buds can also be stored at 10° C. for at least eighteen months with only a slight loss of viability.

After the germinating bulbil has grown for six weeks, the young "axis" or growing rhizome in the center has enlarged sufficiently to be handled. It can be dissected away from the attached scales and killed and fixed for sectioning. Longitudinal sections of this young rhizome show its own apical cell as well as those belonging to the adjacent leaf primordia and the apical cells of roots emerging at the basal end. A particular advantage of this material is that one set of sections will usually provide both transverse and longitudinal cuts of apical cells. These are not, for obvious reasons, always in perfectly vertical or horizontal planes, but most of the sections will be quite usable (Pl. I, Figs. 3-4). Root apical cells with four cutting faces, and stem apical cells with three, can sometimes be found on the same slide.

The procedure used to prepare slides of this material is not difficult to follow. Randolph's modification of Nawaschin's solution as

given by Johansen (1940) yields good fixation in twenty-four hours. Dehydration in tertiary butyl alcohol as recommended by the same author left the material soft enough to cut easily, and embedding in paraffin presented no difficulties. Sections were cut at fifteen microns; twelve would probably be slightly better. Bleaching with hydrogen peroxide before staining tended to improve the preparations. Sections were stained overnight in safranin dissolved in 50 per cent ethyl alcohol, with careful destaining in acidified 70 per cent alcohol. After the completion of the dehydration, they were counterstained for one-half to one minute with fast green dissolved in clove oil. Other combinations of stains, like iron hematoxylin and orange G, would probably give at least equally good results.

This method of preparing apical cell slides is so comparatively simple that it is surprising botanists have not used it more often. Large numbers of ferns produce sporophytic buds of one kind or another which could probably be used (Heinricher, 1878; Kupper, 1906), but most of these species are tropical forms usually available only as herbarium material. Also, in many instances, the buds are either not conspicuous, or are formed on the frond only when it is isolated from the parent plant. According to Sadebeck (1895), *C. bulbifera* is the only fern producing a prominent bud with large fleshy scales containing an abundant reserve food supply. *Phegopteris sparsiflora* Hook. which Sadebeck describes, also has conspicuous pairs of buds at the bases of the pinnae, but this plant appears to be limited to the East African flora. Besides *C. bulbifera*, the only North American species known to this author which produces an evident and accessible bud is *Camptosorus rhizophyllus* (L.) Link., the walking fern, whose fronds root at the tip. According to Kupper, the apical cell of this bud is difficult to demonstrate, although it can be done. Heinricher (1881) and Zimmermann (1881) both describe in detail the development of the bulbil of *Asplenium bulbiferum* Forst., which resembles that of *C. bulbifera* slightly, but is much smaller, and germinates while still attached to the frond. Straus (personal communication, 1951) has shown the writer excellent apical cell preparations from the bulbil of *Dryopteris prolifera* (Retz.) C. Chr., which, like *A. bulbiferum*, is a tropical species. These last two ferns, however, are often found in the United States in botanical-garden collections.

To judge from the extensive literature, all known sporophytic

buds on ferns develop by means of apical cells. These buds represent a greatly neglected source of material for classroom or other demonstrations of the apical cell type of growth, and *Cystopteris bulbifera*, as the most abundant northern hemisphere species with conspicuous adventitious buds, is suggested for preparing slides for this use.

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Cystopteris bulbifera (L.) Bernh

FIG. 1. Side view of a bulbil attached to a frond (scale in millimeters)

FIG. 2. Three bulbils on fronds, very slightly enlarged

FIGS. 3-4. Transverse and longitudinal sections of apical cells $\times 417$

FORESTRY

SOME RESUPINATE POLYPORES FROM THE REGION OF THE GREAT LAKES. XXIII*

DOW V. BAXTER

SURVEYS made from areas bordering the Bering Sea in Alaska to the Baltic Sea in Russia and from the Arctic Ocean to the Caribbean and from Swedish Lapland through most of Europe have resulted in a somewhat better understanding of the relationships and occurrences of the resupinate polypores on both continents. Overholts (11) has stated that at least 43 per cent of the species of the American pileate polyporaceae appear in Europe or in other parts of the Eastern Hemisphere.

Although lists of fungi from Europe and America might correspond in a broad pattern, differences between the floras become more apparent as one acquires an acquaintance with field environments on both continents. It is known, for example, that the almost ubiquitous *Ganoderma applanatum* (Pers.) Pat. grows in both places, but differences in its growth habits in Europe and in North America soon become obvious to the collector. In an afternoon's foray about Ann Arbor, for example, one can scarcely avoid seeing this fungus, and it appears with equal frequency over large sections, especially in the Middle West in this country. With the exception of a comparatively few areas, notably Denmark, I have rarely seen specimens of it in Europe outside herbaria. Another fungus, *Polyporus pargamenus* Fr., is common all over the State of Michigan, but I have never observed it in the territory extending from Lapland and Russia to south Bohemia. In Swedish hardwoods *Fomes robustus* Karst. is present on oak, but it does not occur on hardwoods about Ann Arbor. *Polyporus carneogilvidus* Romell likewise attacks oak wood in Sweden, though it has never been collected here. *Pol. vulgaris* Fr. *sensu* Romell, *Pol. sericeo-mollis* Romell and *F. annosus* (Fr.) Cooke may readily characterize a north European forest-fungus flora of an arboreal type closely related to many of our timberlands in the Upper

* Financial support for several plates presented in this paper has been given by the School of Natural Resources, University of Michigan.

Peninsula. Although *Pol. vulgaris* is represented in such a Michigan forest, it is not so prevalent as in the forests of Sweden about Stockholm.

In North America I have collected *Fomes annosus* in the Tongass National Forest of southeastern Alaska, where it is rather common, and in many regions of this continent, but nowhere in the northern forests of Alaska, Canada, or the United States does it appear as abundantly as in many conifer areas of Europe. Only in southeastern American localities (especially in the Piedmont country) does its occurrence suggest the abundance observed in plantations of Scotland, in many Swedish spruce forests, or those conifer timberlands of south Bohemia. These forests in Europe bear little resemblance to a juniper association of parts of the South Carolinian Piedmont. One is not reminded at all of South Carolina forest sites infested with *F. annosus* when observing stands where root rot appears over vast areas in Sweden or Norway. Certain soil factors and the fact that the land has been under cultivation prior to the present tree occupancy may, however, be analogous for some localities. Furthermore, it would be possible to make a sizable collection of polypores in a few hours from the Gulf States and in the Southeast that would be entirely unlike anything represented in Europe.

This paper discusses a number of North American and European polypores with special reference to their occurrence and distinguishing features. Because usual descriptions of the plants included here do not consider potential variations in appearances of the fruiting bodies when the plant is exposed to different field environments, the polypores are placed in groups 1 to 8 in Table I to facilitate their determination. *Poria flavomarginata* Murr., an allied southern plant, but characterized by minute pore mouths and spore sizes, does not belong to this culture group. It produces a greenish-yellow mycelium (Pl. IX).

Distinctions that pertain only to the significant gross morphological and the microscopic features of the plants are emphasized in the descriptions that follow the table. It is well known that isolates vary in texture and color of the rots even for the same species, but such entities retain their features for indefinite periods in cultures (2). There are, indeed, significant temperature-growth rate characteristics that are often marked. Where these are distinctive, forms (not species) are designated.

TABLE I
OCCURRENCE OF CERTAIN BROWN POLYPORES IN NORTH AMERICA

Fungus	Wood	Form distinguished by response in culture
<i>Fomes Arctostaphyli</i> Long	Arctostaphylos and other desert shrubs
<i>Fomes igniarius</i> (L.) Gill	Populus (aspen), exceptionally on birch*	
<i>Fomes igniarius</i> var. <i>nigricans</i> Fries	Betula, Fagus, Acer, and other woods	. . .
<i>Fomes pomaceus</i> (Pers.) Big. & Guil.	Prunus and others rosaceous hosts	. . .
<i>Fomes pomaceus</i> var. <i>Crataegii</i> (Pers.) Baxter	Crataegus
<i>Poria laevigata</i> (Fr.) Cooke	Betula and other hardwoods
<i>Poria spiculosa</i> Camp. & David.	Carya	<i>f. prunicola</i> comb. nov. on Prunus.
<i>Poria floridana</i> (Murr.) Sacc. & Trott.	Southern woods	Form I on <i>Quercus nigra</i> Form II on <i>Quercus phellos</i> Form III on <i>Carpinus sp.</i>
<i>Poria punctata</i> (Fr.) Cooke	On a great variety of hardwoods, but most common on Alnus, Rhus, Robinia, and Salix	..
<i>Fomitiporia dryophila</i> Murr.	Southern woods	Form I mostly on <i>Quercus virginiana</i> Form II on <i>Nyssa biflora</i> Form III on <i>Liquidambar styraciflua</i>
<i>Fomes robustus</i> Karst.	Quercus and other hardwoods (also conifers in Europe)	<i>f. Tsugina</i> Overh. on <i>Tsuga canadensis</i> and <i>T. heterophylla</i> <i>f. Abietis</i> forma nov. on <i>Abies concolor</i> <i>f. juniperinus</i> forma nov. on <i>Juniperus sp.</i> <i>f. Taxodii</i> Baxter on <i>Taxodium distichum</i>

* See footnote 1, p. 96.

Fomes Arctostaphyli Long (on desert shrubs)

Typical fruiting bodies (Pl. I, Fig. 2) mostly less than 3 cm. broad, occurring on *Arctostaphylos* spp. Setae are not present. The rot does not exhibit distinct lines as does *Fomes igniarius* (13). *Fomes Arctostaphyli* differs culturally from *F. igniarius*, and is culturally and morphologically different from *F. robustus* (6). Differences between *F. Arctostaphyli* and *F. robustus* involve the larger size of the mature fruiting body and the lighter color of the pore mouths of the latter. A trace of red, usually present on the surface of the fruiting bodies of *F. Arctostaphyli*, is not to be seen in *F. robustus*.

Fomes igniarius (L.) Gill (on Populus Group I of Verrall [12])

Typical mature pileus (Pl. I, Fig. 1) larger than 3 cm. broad, mostly less than 15 cm. broad, rimose, on aspen, exceptionally on birch.¹ Pore diameter mostly $100.8\ \mu$ (Verrall), hyphae of context measure $4.45\ \mu$ (Verrall), setae are present. In ten days on malt agar *Fomes igniarius* grew more slowly (mostly less than 40 mm.) than did *F. igniarius nigricans* at the optimum temperature (27.5°C). According to Verrall (12), this fungus produces a methyl salicylate odor in culture, but Nobles (10) says that the odor is slight in some and nonexistent in others.

Fomes igniarius nigricans Fries (on Betula group and species on other hosts, Groups II and III of Verrall [12])

Typical mature pileus (Pls. II, Figs. 1, right, 2, 3; V, Fig. 1; VII, Fig. 2, right) often large, i.e. larger than 3 cm. broad, often as much as 24.5 cm. broad (and therefore definitely larger than *Fomes Arctostaphyli* (Pl. I, Fig. 2) and ordinarily larger than *F. igniarius* (Pl. I, Fig. 1), growing in the eastern part of the continent but not necessarily averaging larger than *F. igniarius* on aspen in the Rocky Mountain areas), chiefly plane to convex, the surface usually cracking somewhat, but not ordinarily becoming rimose; chiefly on birch, beech, and maple.

Pore diameters are about the same for most collections on birch, i.e. $102.9\ \mu$, but are mostly larger on other hosts, $149.2\ \mu$ (12). Hy-

¹ Green standing aspen is by far the most common tree attacked. The only noteworthy exception encountered in the surveys made for this series of reports was in an area of aspen and birch growing on basaltum at the mouth of the Clearwater at the Athabasca River, Alberta, Canada. Here also the birch were seriously infected from the same fungus that was rotting most of the aspen in the stand.

phae of the context are smaller ($3.19\ \mu$) than those of *Fomes igniarius* ($4.45\ \mu$) (Verrall).

Cultures of *Fomes igniarius nigricans* (Pl. X) grow more rapidly than those of *F. igniarius*, but a methyl salicylate odor is not produced.

Fomes pomaceus (Pers.) Big. et Guill. (on Rosaceus hosts, especially Prunus)

Typical mature pileus (Pls. IV; V, Fig. 2) small, often reflexed, mostly less than 3 cm. broad; usually on Prunus in America, but known on other rosaceous hosts.

Fomes pomaceus and *Poria laevigata* are two polypores of this brown group that grow relatively rapidly in culture at 25°C . In culture *F. pomaceus* produces a thin mat that does not peel readily from the agar, whereas the mat of *P. laevigata* is tough and separates easily from the agar (2). A wintergreen odor is distinctive in *P. laevigata*.

Fomes pomaceus differs in its reaction on gallic acid and tannic acid media from *Poria laevigata prunicola*. *F. pomaceus* belongs to group 5,² in which there is no growth or only a trace on gallic acid medium, and on tannic acid a mat of only 25 mm. or less is evident after seven days. In *P. laevigata prunicola* the mat diameters are about equal on both media in a similar period.

Fomes pomaceus Crataegii (Pers.) Baxter³ (on Crataegus)

Typical mature pileus (Pl. III) resupinate with conspicuous gray margins. Growing on Crataegus.

Poria laevigata (Fr.) Cooke⁴ (on hardwoods, especially birch)

Mature fruiting body (Pl. VI, Fig. 1) resupinate and usually growing on birch and often covering 30 cm. or more of the surface of the

² Classification of Davidson, Campbell, and Blaisdell (5).

³ Complete description presented in Paper V of this series, "Some Resupinate Polypores from the Region of the Great Lakes," *Pap. Mich. Acad. Sci., Arts, and Letters*, 19 (1933): 305-332.

⁴ Complete description presented under the name *Fomes igniarius laevigatus* in Paper V of this series (1). Cultures of *P. laevigata*, regardless of their source or type of substratum, show little or no growth at 35°C . In Paper XVI the plant there tentatively named *Fomitiporella floridana* (?) Race I is now identified as *P. laevigata* on Carpinus by means of reactions in culture.

wood. This plant differs from both *Fomes igniarius* and *F. igniarius nigricans* in being resupinate and in having smaller pore mouths. Setae are present in all these plants, but they are infrequent in *Poria laevigata*. This character, however, is only a relative one.

Features observed in cultures will readily separate *Poria laevigata* from *Fomes igniarius* and *F. igniarius nigricans*, and likewise from the species *P. spiculosa* and the form of *P. laevigata*, designated here as *P. laevigata prunicola*. *P. laevigata* (Pl. X) develops more rapidly (41 mm. in two weeks) at 25° and 30° C. than does *F. igniarius nigricans* (24 and 36 mm., respectively, in two weeks), and also produces a denser and lumpier type of mat. *P. laevigata prunicola* grows still more slowly (5 mm. at 30° C.) than *P. laevigata*, and *P. spiculosa* differs from all three in being the only one of the group that grows rapidly at 35° C. (nearly filling the petri dish). Cultures of *P. laevigata* produce a distinct wintergreen odor at 30° C. in 14 days (1, No. XVI; 9; 11).

Poria laevigata forma **prunicola** (Murr.) comb. nov.⁵ (on Prunus)

Mature fruiting body (Pl. VII, Fig. 1) resupinate, often becoming widely effused up to 3 meters. Species of Prunus, rather than of Betula (as in *Poria laevigata*), are common substrata. Morphologically *P. laevigata* and the form on Prunus are similar, but they differ in culture. Setae are infrequent in both *P. laevigata* and *P. laevigata prunicola*, but are usually shorter in the form than in the species *P. laevigata*. *P. laevigata prunicola* produces a red mottled rot in species of Prunus, but no cankers or sterile mycelium appear. Canker formation may result if standing trees are attacked by *P. laevigata*.

In culture the two fungi differ considerably. *Poria laevigata prunicola* (Pl. X) is much lighter in color than *P. laevigata*, and it grows more slowly, especially at 30° and 35° C. In two-week-old cultures *P. laevigata prunicola* grows only 5 mm., with little or no development at 35° C.

Poria laevigata prunicola cultured in gallic and tannic acid media (2) produces a mat of about equal diameters on both media in a seven-day period, whereas in *Fomes pomaceus* there is no growth or only a trace on gallic acid medium, and on tannic acid medium a mat of only 25 mm. or less is evident in a similar period.

⁵ Complete description presented under the name *Poria prunicola* in Paper V of this series (1).

Poria spiculosa Camp. & Davidson differs morphologically from *Poria laevigata prunicola* in its abundant setae. It grows mostly on hickory and, like *P. laevigata*, produces cankers and a sterile mycelium on standing trees.

Poria spiculosa Camp. & David. (on hickory)

Mature fruiting body (Pl. VI, Fig. 2) resupinate, becoming effused up to 1.5 meters on thoroughly decayed logs of hickory and oak, usually associated with trunk cankers or unhealed branch scars. Setae are abundant. For complete description see reference 3 in the literature cited.

In cultures *Poria spiculosa* does not produce a wintergreen odor (characteristic of *P. laevigata*), and the mat formed is tough and leathery. *P. spiculosa* (Pl. X) grows equally well at 25°, 30°, and 35° C., whereas *Fomes igniarius nigricans*, *P. laevigata*, and *P. laevigata prunicola* exhibit little or no growth at 35° C. *P. spiculosa* has much greater development at 30° and 35° C. in two weeks, and grows into a more leathery type of mat than does *P. punctata*.

Although it is convenient to use the kind of wood or substratum on which the fungus is growing as a means for giving these plants a temporary designation in the field (usually birch and maple for *Poria laevigata*, Prunus for *P. laevigata prunicola*, and *Carya* for *P. spiculosa*), cultures are necessary for critical studies.

Poria punctata (Fr.) Cooke⁶ (mostly on alder, sumac, locust, and willow)

Mature fruiting body (Pl. VII, Fig. 3) resupinate, adnate, never loosening from the substratum, often cracking on drying; on willow, poison sumac, locust, and a large variety of hardwoods. Fruiting bodies are characterized by usually being several times laminated and forming a well-defined, more or less orbicular sporophore, i.e. not widely effused in broad plates over the substratum. This fungus is widely distributed over North America, but occurs more abundantly north of the Gulf States.

In culture *Poria punctata*, unlike *P. laevigata*, *P. spiculosa*, and *Fomitiporia dryophila* (a southern plant), exhibits little or no growth at 30° and 35° C., and the mat is more cottony in texture. It differs

⁶ Complete description presented in Paper VII of this series (1).

further from *P. laevigata* in that no wintergreen odor is produced. Cultures of *P. punctata* (Pl. X) and *P. laevigata prunicola* are generally similar in rate of growth and in their temperature for optimum development (25° C.), but *P. punctata* forms a mat much more cottony in texture.

Fomitiporia dryophila Murr.⁷ (mostly on northern live oak)

Mature fruiting body (Pl. VIII, Figs. 1, 2) largely resupinate but usually becoming somewhat ungulate and suggesting the form of an abortive *Fomes*, as in *Fomes robustus*, for example; *F. dryophila* is effused-reflexed in most collections. The fungus is southern in its distribution, occurring on live oak and the southern gum trees. It is usual for the fruiting bodies of *F. dryophila* to occur on dead limbs of standing trees or on trunks of living trees. (Most resupinate polypores of the genus *Poria* occur on fallen timber.)

Fomitiporia dryophila has more of a tendency to become ungulate (Pl. VIII, Fig. 2), a feature that distinguishes it from *Poria punctata* and *P. floridana*. Field collectors will recognize at once that *Poria punctata*, *Fomitiporia dryophila*, and *Fomes robustus* constitute a group of closely related plants that may be arranged in order of their general appearance. Furthermore, these fungi may be arranged by their more or less geographical occurrences or they may be grouped, when broadly interpreted, with reference to their substrata or hosts. A classification based upon habit of growth, geographical occurrence, and substrata or host relationships would result in the following order: *Poria punctata* (a resupinate that is widely distributed from Alaska and the Northwest Territories eastward to Newfoundland and southward through at least eight Canadian provinces and twenty-nine states, including Mississippi, Florida, and Texas; found on sixty-one different species of wood); *Fomitiporia dryophila* (mostly a semi-resupinate plant which is chiefly known from the states that border the Gulf of Mexico; usually growing on oak, mostly on laurel and live oak); and *Fomes robustus* (sometimes semiresupinate, but more often large, ungulate; characteristically occurring on oak, but known on other woods in Europe, including even the conifers if *F. Hartigii* is considered synonymous [see page 105]). A number of American

⁷ Complete description presented in Paper VIII of this series (1). Also see *Fomitiporia Earleae* in the same volume. This species is synonymous with *F. dryophila* and is included in this paper as Forms II and III of *F. dryophila*.

specimens are referred to *F. robustus*. The majority of these, however, are neither as large nor as rimose as the typical European plants. In rimosity it is similar to old North American specimens of *F. Everhartii*.

In culture, *Fomitiporia dryophila* differs from *Poria punctata* in having a definitely less cottony mycelial mat (see Pl. X for mat of *P. punctata* designated as being cottony) and from both *P. punctata* and *Fomes robustus* in having a faster rate of growth at 30° C. Likewise, *F. robustus* is intermediate in its growth rate between the relatively fast *Fomit. dryophila* and the relatively slow *P. punctata*. *P. punctata* has a more cottony mat than the other two fungi. There is no marked difference in color between the isolates of *P. punctata*, *Fomit. dryophila*, and *F. robustus*.

Cultures of *Fomitiporia dryophila* (Pl. XI) grow much more at 30° C., and even at 35° C., and are usually darker, than those of *Poria punctata*. *F. dryophila* produces more growth at 35° C., and the mat is more cottony than that of *Fomes robustus*. Cultures of *P. floridana* nearly fill the petri dishes at 35° C. (in two weeks), whereas those of *F. dryophila* do not.

Poria floridana (Murr.) Sacc. and Trott.⁸ (on southern woods)

Mature fruiting body (Pl. XII, Figs. 1, 2) resupinate, effused up to 45 cm., the pore surface exhibiting a sheen (velvety appearance and refracting light [glistening] much as does that of *Fomes Everhartii*). This feature is not striking in specimens of *Fomitiporia dryophila*. *Poria floridana* grows on logs of oak, red gum, and *Carpinus*, and, like *F. dryophila*, is apparently more common in the South. The tubes are whitish-stuffed in *P. floridana*, rather than yellowish-stuffed, as described for *F. dryophila*.

This species strongly resembles *Poria melleopora* (Murr.) Sacc. and Trott. It differs in not having pale brown spores, as does *P. melleopora*, and Lowe (9) adds that the hyphae of the subiculum are smaller.

Poria floridana, like *P. spiculosa*, grows almost equally well at 25°, 30°, and 35° C. (27, 28, 21 mm., respectively, in two weeks), but the mat is more cottony in appearance and does not fill the dish as rapidly as does *P. spiculosa* (which grows about 41 mm. in two

⁸ Complete description presented in Paper IX of this series under the name *Fomitiporella floridana* Murr. (1).

weeks). *P. floridana* (Pl. XIII)) grows more rapidly at 35° C. in two weeks than does either *Fomitiporia dryophila* or *Fomes robustus*.

Fomes robustus Karst.⁹ (on oak, other hardwoods, and conifers)

Mature fruiting body (Pls. XIV; XV, Fig. 1) ungulate to appunate, up to 15 cm. broad, smooth, on birch and oak (and other hosts, including conifers, at least in Europe). *Fomes robustus* differs from *F. igniarius* in that its tubes are not whitish-stuffed, but are golden brown.

Cultures of *Fomes robustus* (Pl. XVII) may be distinguished from those of *Poria laevis* by the rate of development at 25° C. (*F. robustus*, 24 mm.; *P. laevis*, 41 mm. for two weeks) and by the mat formation, which is more cottony than that of *P. laevis*. (Growth of *F. robustus* cultures may be variable at 30° C.) *F. robustus* differs from *P. spiculosa* at 35° C. because it shows little or no growth, whereas *P. spiculosa* nearly fills the petri dish at that temperature.

Fomes robustus develops more rapidly and with more luxuriant mycelium than does *F. robustus Tsugina* (6, 7, and 0 mm. at 25°, 30°, and 35° C. for two weeks). It differs in rate of growth from *Poria floridana* and *Fomitiporia dryophila*, both of which produce a larger mycelial mat at 35° C. in two weeks. The rate of development at 30° C. (20 to 41 mm.) will serve as a means by which it may be separated from *P. laevis prunicola* (3 to 5 mm.).

Fomes robustus Karst. *Tsugina* Overh.¹⁰ (on hemlock)

Mature fruiting body (Pl. XV, Fig. 2) resupinate, becoming broadly effused, usually on hemlock. Mouths are whitish-stuffed, whereas those of *Fomitiporia dryophila* are ferruginous. This fungus becomes much more effused over the substratum than does *Poria punctata*.

Cultures of *Fomes robustus Tsugina* (Pls. XVII; XVIII) do not develop as fast at 25° and 30° C. (5 and 7 mm., respectively) as do those of *F. robustus* (which grows at least 20 mm.). Since *F. robustus Tsugina* does not produce mycelial growth at 35° C., it may be separated from other fungi that do (*Fomitiporia dryophila*, *Poria floridana*, *P. punctata*, *P. laevis*, and *P. spiculosa*). Neither *F. igniarius nigricans* nor *P. laevis prunicola* exhibits growth at 35° C., but

⁹ Complete description presented in this paper, page 103.

¹⁰ Complete description presented under the name *Poria tsugina* in Paper V of this series (1).

both have much more luxuriant mycelial formation at 25° C. than does *F. robustus Tsugina*.

Fomes robustus Abietis forma nov. (on the true firs)

Mature fruiting body resupinate, resembling *Fomes robustus Tsugina*, but found on species of *Abies*.

Cultures of *Fomes robustus Abietis* (Pl. XVIII) may be distinguished from all other fungi in this group by the unusual growth pattern, viz., 1, 15, and 0 mm. at the end of two weeks at 25°, 30° and 35° C.

Fomes robustus forma **juniperinus** comb. nov. (on juniper)

Morphologically *Fomes robustus juniperinus* (*Fuscoporia juniperina* Murr.) resembles *F. robustus* forma *Taxodii* (Pl. XVI, Figs. 1, 2). The two are considered identical species in this paper, but the form names are retained. On the basis of present knowledge of *F. robustus* it appears that races do exist. It is known that cultures of isolates from hemlock (both *Tsuga canadensis* and *T. heterophylla*) in many widely separated regions differ from cultures obtained from the fir isolate (*Abies concolor*) in both rate of growth and mycelial features.

The forma "Taxodii" occurs so much more commonly than the one on juniper that it appears that two possible forms or races, "juniperinus" and "Taxodii," may exist. At least they are kept separate until evidence shows them physiologically alike in their responses. If it is determined later that the reactions are similar in culture, the name "juniperinus" will be recognized, since it was established earlier than "Taxodii."

Fomes robustus forma *Taxodii* Baxter¹¹ (on bald cypress)

See discussion under *Fomes robustus juniperinus*.

Fomes robustus Karst., Finl. Bas. in Bidr.
Finl. Nat. o. Folk., 48: 467. 1889

Plate XIV

Fomes igniarius var. *Pinuum* Bres., Rev. Myc., 12 (47): 105. 1890.

Fomes Bakeri (Murr.) Neuman, Bull. Wis. Geol. and Nat. Hist. Surv., 33: 168, t. 6, f. 27a, p. 170; t. 7, f. 27b-d. 1914.

¹¹ Complete description presented in Paper XVIII of this series (1).

Fomes igniarius Abietinus ex Lloyd in Synopsis of the Genus Fomes, p. 243. Cincinnati, 1915.

Fomes setulosus Lloyd. Syn. Fomes, p. 243 (ex Lloyd). 1915.

Fomes robustus var. *Pinuum* Bres. Icon. Myc., Tabula 993. 1931.

Fomes aestriplex Ernst. H. L. Krause, Basidiomycetum Rostochiensium, Supplementum Tertium, No. 404 (according to exsiccati). Teste Kavina et Pilát, Atlas des Champignons de l'Europe. 1936.

Ochroporus robustus (Karst.) Schroet. ex Donk in Rev. der Niederländischen Homobasidiomycetae, No. 9: 248. 1933.

Phellinus robustus (Karst.) Bourd. et Galz. in Bull. Soc. Myc. Fr., 41: 188. 1925.

Phellinus robustus var. *Hartigii* (All. & Sch.) in Bourdot et Galzin, pro parte, Hymen. de Fr. 617. 1928.

Placodes roburneus Quélet, Fl. Myc., 400. 1888 (non Fries). Teste Kavina et Pilát, Atlas des Champignons de l'Europe. 1936.

Placodes Hartigii (All. & Sch.) Huber in Ztschr. f. Pflanzen., p. 4. 1927.

Polyporus Hartigii All. & Sch., Fungi Bav. ex Cent. 1, No. 48. 1890.

Pyropolyporus Bakeri Murr. North Am. Fl., 9: 104. 1908. Teste Kavina et Pilát, Atlas des Champignons de l'Europe. 1936.

Pyropolyporus Robinsoniae Murr. (ex Bres.). North Am. Fl., 9: 108. 1908.

Fructification sessile, woody, compressed-ungulate to applanate, 3-9 × 3-15 × 2-4 cm.; surface smooth, at least scarcely rimose, two or three times deeply sulcate, at first "snuff brown," "wood brown" becoming gray or black, i.e. "drab," "hair brown" to black; margin thick, broad, rounded, smooth; context zonate, glistening brown, "clay color," 0.5-2 cm. thick; tubes stratified, more or less whitish-stuffed in the older layers, 1-5 mm. long each season; mouths mostly 5-6 to a mm., edges entire; basidia 10-15 × 7-10 μ; spores smooth, hyaline, globose, 5-7 μ; setae none; hyphae seldom branched, brown, 2.5-5 μ in diameter.

Forms.—*Fomes robustus Tsugina* Overh. (= *Fomitiporia tsugina* Murr. North Am. Fl., 9: 9. 1907. *Poria tsugina* (Murr.) Sacc. and Trott. in Sacc., Syll. Fung., 21: 332. 1912.)

Fomes robustus Abietis forma nov. (= *Fomes robustus Tsugina* on *Abies concolor*).

Fomes robustus juniperinus forma nov. (= *Fuscoporia juniperina* Murr. North Am. Fl., 9: 4-5. 1907).

Fomes robustus Taxodii Baxter (Pap. Mich. Acad. Sci., Arts, and Letters, 37: 193-194. 1946).

Allied species.—*Fomes robustus* is likely to be mistaken for *F. Everhartii*. The presence of the conspicuous setae in *F. Everhartii* will enable one to distinguish between the two fungi. In North

America the resupinate or semiresupinate form *Tsugina* is generally similar except in habit of growth. My experience with *F. robustus* in Europe has been with the species on oak, but it is reported on pine, spruce, and fir from that continent. Lloyd (7) holds that, notwithstanding the vastly different host for *Fomes Hartigii* (the silver fir, *Abies pectinata*), *F. Hartigii* and *F. robustus* appear to be the same in all characters. On the other hand, Lohwag (8) believes that the fungus on conifers in Europe is *F. Hartigii*. He states that *F. robustus* occurs exclusively on oaks and chestnuts, whereas *F. Hartigii* grows only on coniferous wood. Lohwag reports that *F. robustus* in time develops some fissures on the surface of the fruiting body and that these are seldom present in *F. Hartigii*. He finds that the fruiting bodies of *F. Hartigii* are generally smaller than those of *F. robustus*. Characteristic of the fruiting bodies of *F. Hartigii* are the numerous pits on the surface of the pileus that are caused by drops of water. These, he states (8), are seldom observed in *F. robustus*.

It is pointed out that tube development in *Fomes Hartigii* begins relatively late, and, in contrast to *F. robustus*, the layer of tubes does not develop directly a new tube layer. Instead, rather thick layers of trama occur between the rows of tubes. A further distinction between the two plants is made with reference to the mode of attachment of the fruiting body to the tree. *F. Hartigii* is mounted with its entire base upon the substratum, whereas *F. robustus* breaks out from the wood with its younger part, and only the most recently developed part lies just outside the bark. Therefore, large fruiting bodies of *F. robustus* are to be separated from their substratum without too great difficulty—and only a small place of attachment is pulled away. *F. Hartigii*, on the other hand, can be taken off in its entirety. *F. robustus* appears to grow faster.

In North America the form *Tsugina* commonly grows in a resupinate condition on both eastern and western hemlock, but there is little morphological difference to be noted between *Fomes robustus Tsugina* and the species on oak in Europe. The form, however, is not the same physiologically, although resemblances in color and formation of wavy brown lines in cultures can often be seen. Although the lines formed in *F. robustus* are more conspicuous than those in *F. robustus Tsugina*, the chief difference

between the plants is in their varying rate of growth in culture. *F. robustus* develops about twice as fast as *F. robustus Tsugina*.

Fomes robustus and *F. rimosus* may be confused. The smoother pileus of *F. robustus* should enable one to distinguish the two plants. The spores are brown in *F. rimosus* and hyaline in *F. robustus*.

Fomes igniarius is readily distinguished from *F. robustus* by the fact that the tubes in *F. igniarius* are whitish-stuffed instead of being golden brown.

Fomes torulosus (*F. rubriporus* Quélet), referred to by Lloyd (Fomes), belongs in this general group of plants. It has been called *Fomes fuscopurpureus*, according to him, and *Fomes rubriporus* by Boudier and Quélet. He states that he has a collection on oak from Louisiana, and that the fungus is not rare about Paris, but it is not known from England. There is a collection known from Japan, and it is probable that it will prove "to be more common in the Tropics when the distribution is better known" (7). The fungus is mentioned here because of the Louisiana record of occurrence. The fructification is described as applanate, sometimes thin, an inch or less, or other specimens 3-4 inches thick. The surface is soft when young, pubescent, at length with concentric raised, soft ridges, often with an obtuse inflated edge; context light brown (ochraceous tawny); pores minute, the tissue concolorous with the context, but the mouths at first purplish, losing the color when old and becoming brown; spores hyaline, globose, 4-5 μ ; abundant setae, projecting 16-20 μ . Habitat index.—*Betula lenta*, *B. lutea*, *B. nigra*, *B. papyrifera occidentalis*, *Eucalyptus globulus*, *Lysiloma candida*, *Populus* spp., *Quercus borealis*, *Q. marilandica*, *Q. nigra*, *Q. texana*, *Robinia* spp., *Salix* spp., *Taxus brevifolia*.

f. *Tsugina*.—*Picea sitchensis*, *Pinus* spp., *Pseudotsuga taxifolia*, *Tsuga canadensis*, *T. heterophylla*, *T. Mertensiana*.

f. *Abietis*.—*Abies balsamea*,¹² *A. concolor*, *A. lasiocarpa*,¹² *A. nobilis*.¹²

¹² Originally listed under *Fomes robustus Tsugina*. The isolates have not been tested in culture to match that from *Abies concolor*, which shows distinct reactions in culture from *F. robustus Tsugina*.

f. *juniperinus*.—*Juniperus virginiana*.¹³

f. *Taxodii*.—*Taxodium distichum*.¹³

Distribution.—British Columbia; California, District of Columbia, Georgia, Indiana, Louisiana, Maine, Maryland, Minnesota, Missouri, New Jersey, Ohio, Oregon, Pennsylvania, Texas, Virginia, Wisconsin.

f. *Tsugina*.—Alaska; British Columbia, Ontario, Quebec; California, Colorado, Connecticut, Idaho, Maine, Massachusetts, Michigan, New Hampshire, New Jersey, New Mexico, New York, North Carolina, Ohio, Oregon, Pennsylvania, Tennessee, Vermont, Wisconsin, Washington.

f. *Abietis*.—Colorado.

f. *juniperinus*.—Arkansas, Louisiana.

f. *Taxodii*.—Georgia.

Occurrence.—*Fomes robustus* is fairly common in Europe on oak. Lloyd (7) reports it from Australia, Hawaii, and Japan.

f. *Tsugina*.—Common in regions where hemlock grows.

Cultures.—Isolated from *Betula nigra*, Great Falls, Virginia. One-year-old wood-block cultures of *Fomes robustus* mask both red-gum and white-pine test pieces with such a luxuriant growth of mycelium that the shape of the wood blocks is concealed. In luxuriant growth, color, and black line formation, cultures chiefly resemble those of *F. Everhartii*, but, unlike that species, plugs of mycelium are not formed by *F. robustus*.

Wood block cultures of *Fomes robustus* also resemble those of *Poria punctata*, and they suggest somewhat those of *Fomes nigro-limitatus*, *P. laevigata prunicola*, *P. spiculosa*, *Polyporus texanus*, *P. floridana* Race III on *Carpinus*, *Fomitiporia dryophila* Race II on *Nyssa biflora*, *Poria laevigata* on *Carpinus*, and the forma *F. robustus Tsugina*. Petri-dish tests made at different temperatures may be used, together with texture features, to distinguish *F. robustus* from *P. punctata*. See page 109.

Decay.—A yellow trunk rot is produced, which, according to Cartwright and Findlay (4), is mainly confined to the sapwood, but extends into the heartwood. The rotted part is usually surrounded by a narrow dark-brown zone of incipient decay. The

¹³ See comments in text, p. 103.

TABLE II

MYCELIAL GROWTH CHARACTERISTICS OF *FOMES ROBUSTUS* AND SPECIES THAT RESEMBLE THIS FUNGUS MOST CLOSELY IN CULTURE*

Name	Rate of growth in mm. of 14-day-old petri-dish tests			Features in one-year-old wood-block tests.
	Centrigrade			
	25°	30°	35°	
<i>F. robustus</i> <i>Betula nigra</i> Virginia	24	33	1	In luxuriance of color and mycelial growth this fungus resembles <i>F. Everhartii</i> most closely. No mycelial plug forms in flasks with cotton stoppers. Best distinguishing features are exhibited in petri-dish temperature series.
<i>F. robustus</i> <i>Quercus</i> sp. Sweden	22	15	1	
<i>F. robustus</i> <i>Tsugina</i> <i>Tsuga heterophylla</i> British Columbia	6	7	0	Isolates from both <i>Tsuga canadensis</i> and <i>T. heterophylla</i> are generally similar in appearance. The form differs from the species in rate of growth as well as in being much less luxuriant in mycelial production.
<i>F. robustus</i> <i>Tsugina</i> <i>Tsuga canadensis</i> Michigan	4	8	0	
<i>F. robustus</i> <i>Abietis</i> <i>Abies concolor</i> Colorado	1	15	0	Differs from isolates of <i>Tsugina</i> in its unusual rate of growth. Intermediate between the species and f. <i>Tsugina</i> in luxuriance of mycelium, but otherwise similar.
<i>F. nigrolimitatus</i> <i>Tsuga heterophylla</i> Alaska	0	0	0	Differs from other members of the group in its exceedingly slow growth.
<i>F. Everhartii</i> <i>Quercus imbricaria</i> Michigan	24	35	5	Mycelial plugs formed in flask cultures with cotton stoppers. These do not appear with <i>F. robustus</i> .
<i>F. Everhartii</i> <i>Quercus</i> sp. Oklahoma	28	33	4	The description is like that given for <i>F. robustus</i> on <i>Betula nigra</i> .

TABLE II (Concluded)

Name	Rate of growth in mm. of 14-day-old petri-dish tests			Features in one-year-old wood-block tests.
	Centigrade			
	25°	30°	35°	
<i>Poria punctata</i> <i>Rhus vernix</i> Michigan	24	3-10	0	Differs from <i>F. robustus</i> in its growth rate at 30° C.†
<i>P. laevigata prunicola</i> Black cherry Michigan	28	3-5	0	Rate of growth at 30° C. will separate this fungus from <i>F. robustus</i> .†
<i>Poria spiculosa</i> Hickory Pennsylvania	41	41	37	Differs from <i>F. robustus</i> in growth rate at 25° C.†
<i>Poria floridana</i> Strain III <i>Carpinus</i> sp. Louisiana	41	41	41	Differs from <i>F. robustus</i> in growth rate at 35° C.†
<i>Fomitiporia dryophila</i> Strain II <i>Nyssa biflora</i> Florida	30	38	18	Mycelium much more whitish or whitish buff as well as "cream buff." One-year-old cultures of <i>F. robustus</i> are uniform in color.
<i>Poria laevigata</i> <i>Carpinus caroliniana</i> Virginia	41	41	1	Differs from <i>F. robustus</i> in its growth rate at 25° C.

* In the tests different cultures vary slightly in their measurements for each temperature, but the relative growth expressed remains more or less constant.

† In this group mycelial wood-block cultures are not so useful for distinguishing purposes as are petri-dish temperature tests.

area attacked is usually limited to within about a yard on each side of the fruiting bodies.

Fomes robustus, like a large number of the brown resupinate polypores, grows relatively slowly in culture, as indicated in Table

II. No clamp connections are formed. The fungus exhibits a strong reaction with tannic acid medium.

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FIG. 1



FIG. 2

FIG. 1. *Fomes ignarius* on aspen, Placitas, New Mexico (courtesy of U. S. Division of Forest Pathology)

FIG. 2 *Fomes Arctodaphyl* on manzanita, Klamath Falls, Oregon



FIG. 1 Ungulate fruiting body of *Fomes igniarius* (left), Fairbanks, Alaska. Convex structure of *F. igniarius nigricans* (right) on birch, Selkirk, Yukon Territory. Mature fruiting bodies of *F. igniarius* are usually smaller than those of *F. igniarius nigricans*.



FIG. 2

FIG. 3

FIG. 2 *Fomes igniarius nigricans* on *Alnus sinuata*, Valdez, Alaska

FIG. 3 *F. igniarius nigricans* growing in form similar to that of *Poria laevigata prunicola*. On yellow birch, Edmunston, New Brunswick



Fomes pomaceus (*Crataegus* sp., Ann Arbor, Michigan. Note the characteristic margins and compare them with those of *F. pomaceus* (Pl. IV) and the "resupinate" *F. ignarius nigricans* (Pl. V, Fig. 2)



FIG. 1



FIG. 2



FIG. 3

Various forms of *F. pomaceus* (all specimens from Clermont Co., Ohio)

FIG. 1. Effused-reflexed form on wild plum

FIG. 2. Resupinate form on wild plum, fruiting body several years old

FIG. 3. Resupinate form on peach; fruiting body approximately one year old



FIG. 1

FIG. 1. *Fomes ignarius nigricans* on willow, Valdez, Alaska
Crataegi (Pl. III) This growth is especially common for the species in the North



FIG. 2

Note its similarity in growth appearance to *F. pomaceus*
 FIG. 2. *F. pomaceus*, Dismal River, Nebraska National Forest, Halsey, Nebraska



FIG. 1 *Poria laevigata* on upright yellow birch trunk, Chelsea, Michigan



FIG. 2 *Poria spiculosa* on Hickory, Crossett, Arkansas



FIG. 1

FIG. 1 *Poria laerigata prunicola* on *Prunus* sp., Gander Lake, Newfoundland

FIG. 2

FIG. 2 *Poria laerigata* (left side) and *Fomes ignarius nigricans* (right side) on same log, St. Demase, L'Islet Co., Province of Quebec

FIG. 3

FIG. 3 *Poria punctata* on alder, Gander Lake, Newfoundland

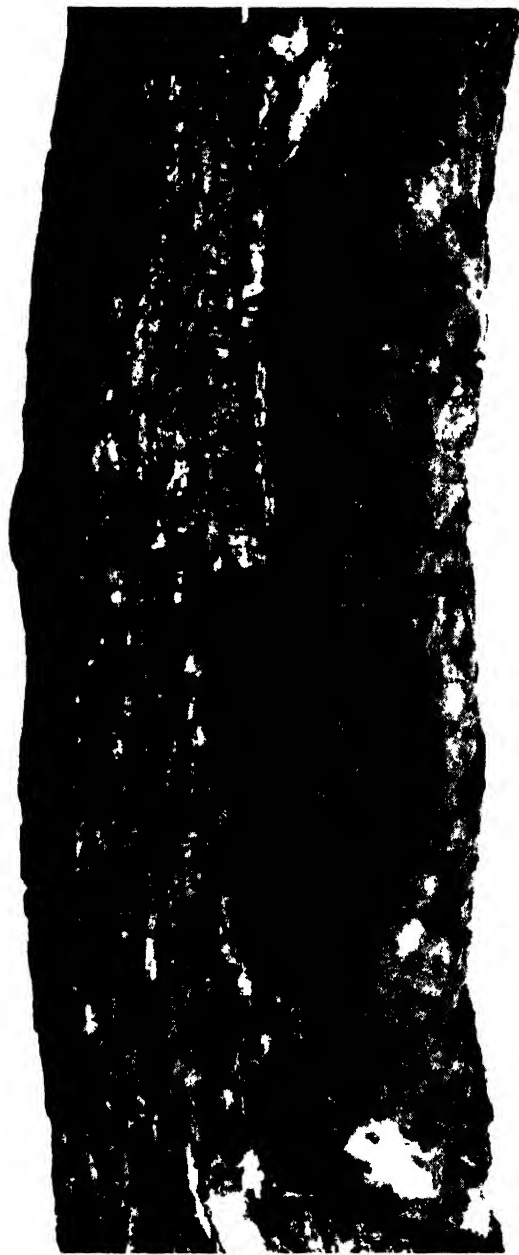


FIG. 1

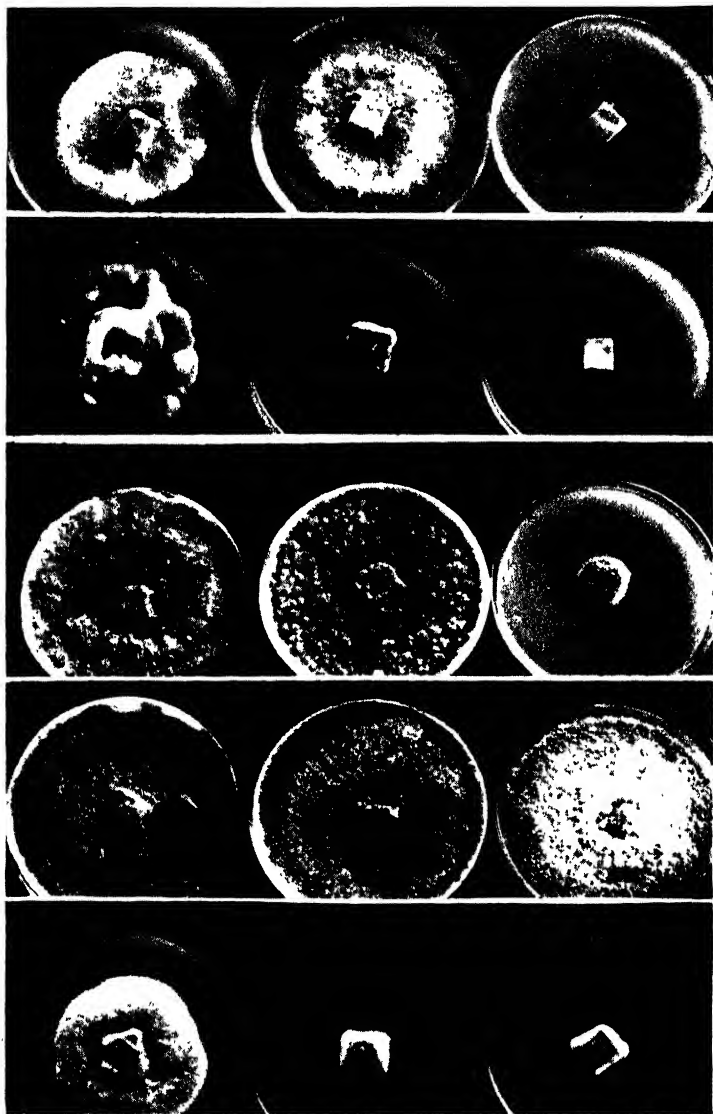


FIG. 2

FIGS. 1-2. Resupinate and effused reflexed fruiting bodies of *Fomitiporia dryophila* on *Quercus virginiana*, Logtown, Mississippi



Poria flatomarginata on *Salix* sp., Everglades, Florida. This plant is readily distinguished by its greenish-yellow mycelium in culture



Cultures of *Fomes* and *Poria* kept at 25°, 30°, and 35° C. for fourteen days, listed in order from top to bottom:

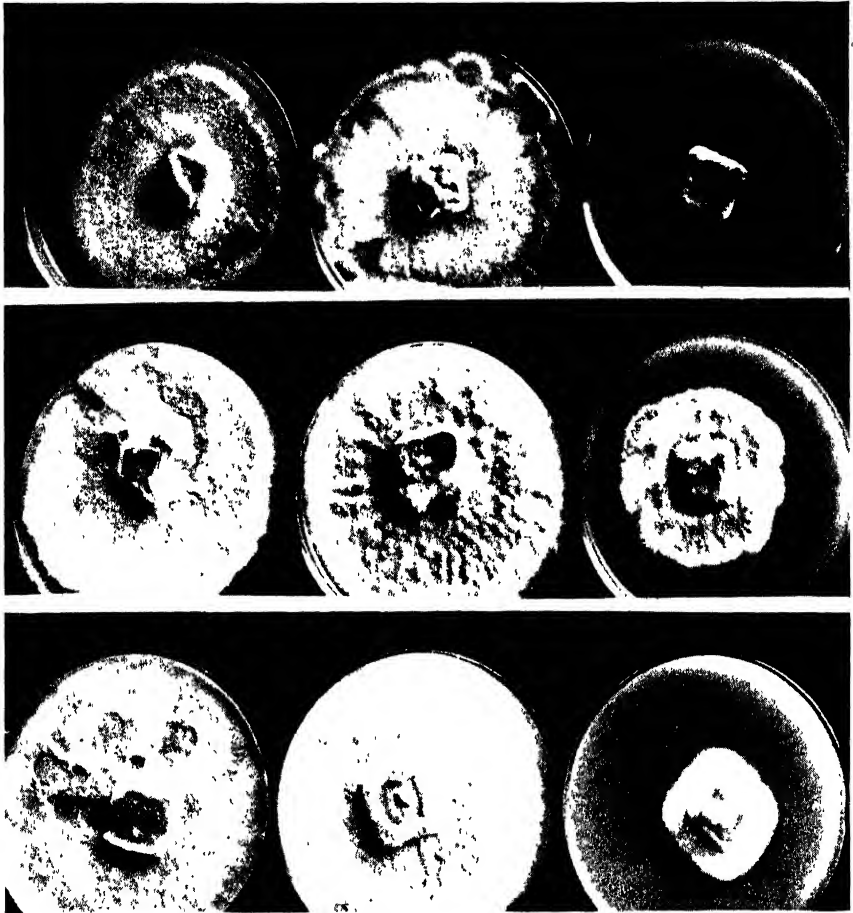
Fomes ignarius nigricans X on *Betula kenaiensis*, Moose Pass, Alaska

Poria laevigata prunicola on *Prunus serotina*, Grand Island, Michigan

P. laevigata on maple, Munising, Michigan

P. spiculosa on *Carya* sp., Saltsburg, Pennsylvania, U. S. Division of Forest Pathology

P. punctata on *Rhus vernix*, Ann Arbor, Michigan



Cultures of *Fomitiporia dryophila* kept at 25°, 30°, and 35° C for fourteen days, listed in order from top to bottom. Form I on *Quercus* sp., Ocala National Forest, Florida, Form II on *Nyssa biflora*, Osceola National Forest, Florida, Form III on *Liquidambar styraciflua*, Kingsland, Georgia

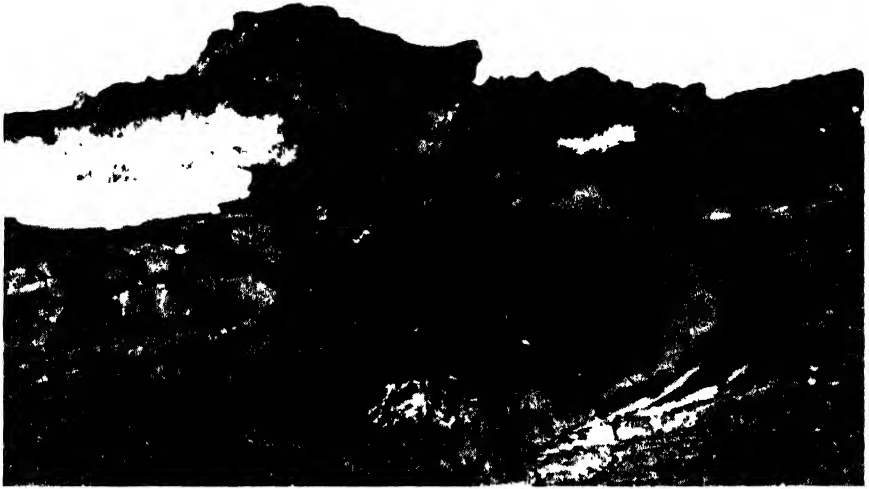
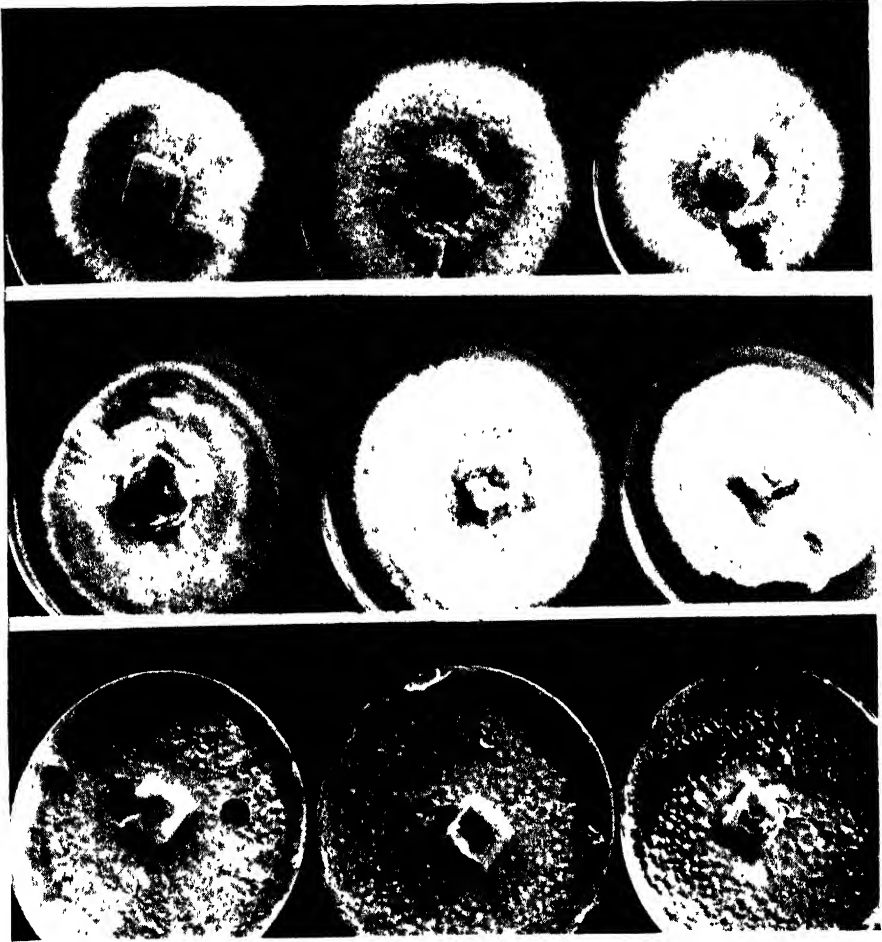


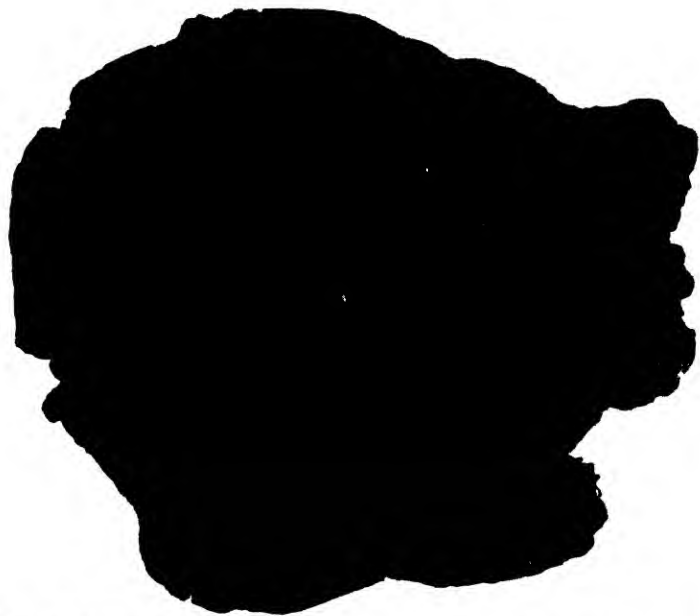
FIG. 1 *Poria floridana*, Form I on *Quercus nigra*, Waterboro, South Carolina



FIG. 2 *P. floridana*, Form III on *Carpinus*, Franklinton, Louisiana



Cultures of *Poria floridana* kept at 25°, 30°, and 35° C. for fourteen days, listed in order from top to bottom: Form I on *Quercus nigra*, Waterboro, South Carolina; Form II on *Quercus phellos*, Little Rock, Arkansas; Form III on *Carpinus* sp., Franklinton, Louisiana



Decayed oak wood and fruiting body of *Fomes robustus*, Stockholm, Sweden



FIG. 1 *Fomes robustus* on *Betula nigra*, Great Falls, Virginia



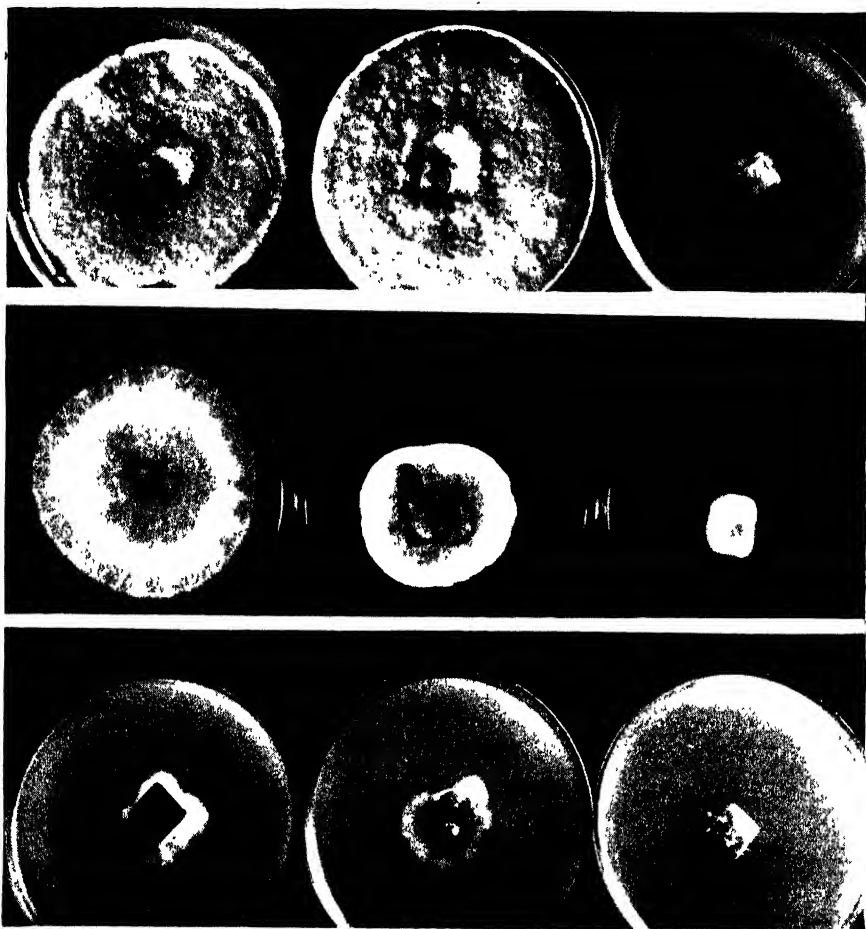
FIG. 2 *F. robustus Tsugana* on *Tsuga canadensis*, Wisconsin Dells, Wisconsin



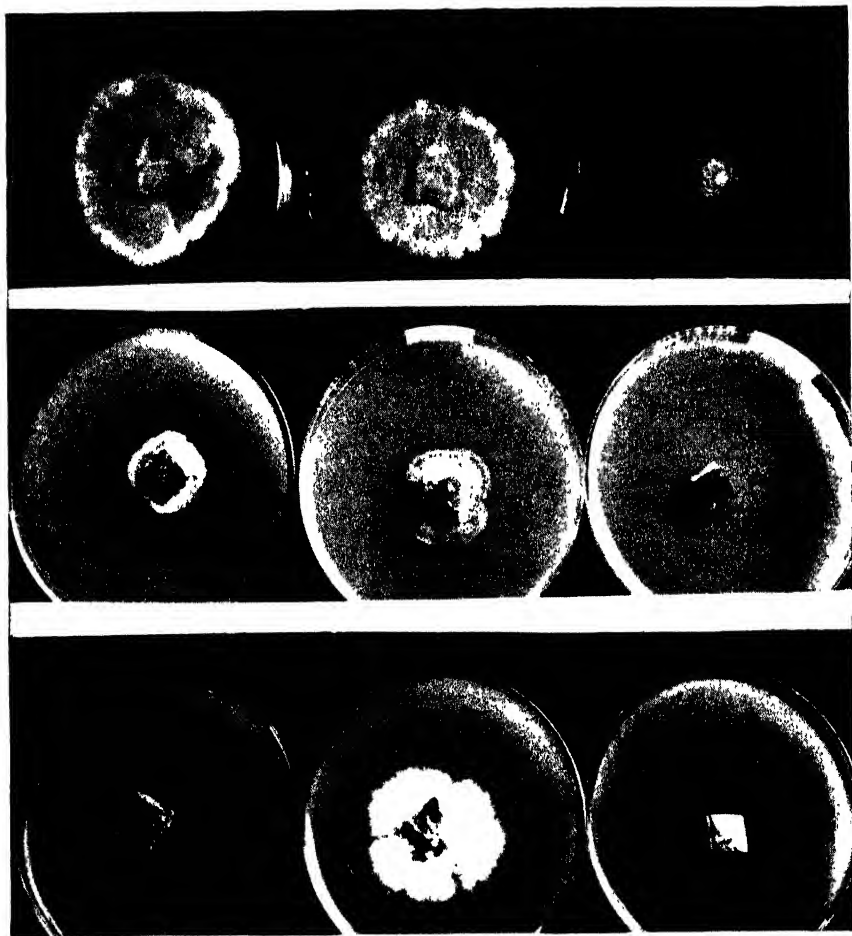
FIG. 1 *Fomes robustus Tarodii* on *Tarodum distichum*, Okefinokee Swamp, Georgia



FIG. 2 *Fomes robustus Tarodii* on *Tarodum distichum*, locality unknown, Arkansas (formerly designated *Fuscoportia juniperina* Murr.; discussed in Paper XII of this series, 1)



Cultures of *Fomes* kept at 25°, 30°, and 35° C for fourteen days, listed in order from top to bottom: *Fomes robustus* on *Betula nigra*, Great Falls, Virginia; *Fomes robustus*, culture from Stockholm, Sweden; *Fomes robustus* *Tsugina* on *Tsuga canadensis*, Marquette National Forest, Michigan



Cultures of *Fomes* kept at 25°, 30°, and 35° C. for fourteen days, listed in order from top to bottom:

F. robustus *Tsugina* on *Tsuga canadensis*, Norfolk, Connecticut, culture supplied by J. S. Boyce

F. robustus *Tsugina* on *Tsuga heterophylla*, Vancouver, British Columbia

F. robustus *Abietis* on *Abies concolor*, Sangre de Cristo Range, Colorado

THE FOREST INDUSTRY'S COÖPERATIVE RESEARCH PROGRAM

BRUCE G. BUELL

THE wood-using industries of the Lake States are definitely past the stage at which they can look to new sources of timber to keep them supplied with their annual needs. The original reserve of virgin timber is rapidly vanishing. Owners who have big investments in wood-using plants and equipment have of late years become increasingly aware of this situation. It is a plain economic fact that, as long as there is a plentiful supply of any commodity at hand, people will not (under keen competition cannot) incur expenses to replenish or safeguard that supply. I find that the majority of owners do not have the advantage of the long-term viewpoint which is drilled into us as foresters. Therefore many of them have not been as foresighted as they should be, but now, with clear evidence before them that this unlimited reserve of timber is vanishing, most owners are thinking in terms of growing timber—some, of growing it on their own lands, others, of letting someone else grow it, but all have the growth factor uppermost in their minds.

Twenty years ago industrial forestry in the Lake States was practically nonexistent; probably not over 100,000 acres of industry-owned forests were under management. It has been only during the past ten years that industrial forests have been developed to the point where they have become a major factor in our overall scheme of forest management. Today a quick survey of the eleven pulp and paper mills mentioned later in this paper indicates an ownership of 1.5 million acres. In addition, there are other pulp and paper mills, sawmills, mining companies, and many smaller owners not included in this survey, so that it seems safe to say that there are 3 to 4 million acres of industrial forests in the Lake States now under systematic forest management. The exact figure is not important. It is significant that the acreage is substantial and rapidly increasing.

When the management of a paper mill has to face the problem of

owning lands and growing timber crops, it considers two questions: (1) Must it do so in order to get the wood it needs? (2) How much will it cost per cord?

With regard to the first question, let us look at the landownership pattern first. The following figures are taken from a recent publication of the Forest Service—*Forest Resources of the Lake States Region* (1950), by R. N. Cunningham and the Staff of the Lake States Forest Experiment Station. We find that of 50 million acres of forest land in the Lake States 7 million are owned by the Forest Service, 8 million by the States, and 6 million by the counties—a total of 21 million. Of the remaining 29 million, 14 million are in “farm woods.” Presumably much of this acreage consists of woodlots in the southern parts of the States and is in hardwoods. In any case, the farm woodlots have the poorest management, and the lowest growth rate of all the classes of forest ownership. Also, a very high percentage of the yield of these woods is used locally, either by the owner or by his neighbors, so that for the most part they can be eliminated from the picture so far as production of pulpwood is concerned. This leaves us with only 15 million acres available for industry and private ownership of all kinds, and of this amount 3 million acres are already owned by pulp mills.

Cunningham states that we may expect a growth of about one sixth of a cord (16 cu. ft.) per acre per year for the next twenty years. He also says that only 26 per cent of the present use of forest production is in the form of pulpwood. Hence pulp mills will grow approximately 500,000 cords of wood on their own lands, of which 130,000 will be pulpwood. On the 12 million acres of private land we may expect 2,000,000 cords, of which 520,000 will be pulpwood. On the 22,000,000 acres of land in public ownership we may expect 3,700,000 cords, of which 960,000 will be pulpwood. Thus we have a total growth of 6,200,000 cords, of which 1,620,000 can be allotted to pulp mills if we assume that present-day consumption of all forest products continues unchanged in comparative percentages and in species.

The consumption of pulpwood produced in the Lake States amounts to about 1,700,000 cords. I do not want to go into this situation in detail, but I use this merely to point up the fact that our total growth will just about take care of the total drain on pulpwood, with nothing to spare unless we switch to other species, or raid the

supplies now going to other industries, or practice closer utilization. This emphasizes the necessity of doing all we can to step up growth on all lands, public and private, to meet future demands. It also shows very vividly that competition for wood will be keen; and when it is keen, the production from public lands cannot be depended on to sustain any given plant. The only way publicly owned timber can be sold is to the highest bidder. Thus a manufacturer who can make a high profit from his finished product can and will bid higher for stumpage than a competitor who has a lower profit. Market conditions change rapidly and so do profit margins. No one of sound mind would consider a big investment in a plant without assured stability of the supply of his raw material. This assurance the public agencies cannot give; therefore a certain amount of ownership by industry is a "must."

Let us take up the second point, the cost of producing wood on industry-owned land. This is a matter for a cost-conscious forester to work out. His primary consideration must be that his company needs all the wood which he can produce. If he is to be successful, he must then produce that wood at a cost that will not be out of line with what similar wood brings in the open market. What measures can he take and what expense may he incur and still accomplish this?

First of all, the forester has to evaluate the carrying costs of his land. Annual taxes and protection and administrative costs are constants, but are rising steadily as our dollar value drops. It costs just as much to carry an acre of idle land as an acre of good growing timber. He must therefore get his idle land to working. He will also have some lands which are poorly stocked, others growing species of low value, or species which are of no use to his particular industry. He will have swamps that are stagnant and stands of reproduction too thick for good growth. He is faced with problems of excessive loss through fire, disease, insect attack, windstorms, and ice and snow storms, all of which cut into the growth rate for his property. He will have other areas that do not reproduce well after cutting. His problem is to do what he can to combat all these adverse factors and still show a net profit for his operations.

During the past few years stumpage values have risen along with labor costs and everything else. This has given our management

forester opportunities to practice some silviculture that has been impossible in past years, and still keep his figures on the ledger in ink of the proper color.

But what measures is he to take, and what will give the best results per dollar spent? A few of us have been industrial foresters for twenty years, and many more for lesser periods. Upon comparing notes we find that we disagree on almost every point save one. That one is that "we don't know." These silvicultural methods are rapidly becoming of more importance to us. In our search for the answers we find that the Forest Experiment Station has done a great deal of work; the various schools and other agencies have done some. But much of it has been concerned with sawlogs, particularly hardwoods, and a large part of the information published has been based on small-scale experiments, which are necessarily limited in scope and hence lack region-wide accuracy.

During the past few years nearly every one of the major pulp and paper companies has done some practical research on its own lands. This work has varied widely, depending on the needs of the company and the individual ideas of the foresters in charge. Much of it has duplicated that done elsewhere, a large portion of it has been incomplete, and very few of the results have been made available to others. Thus the need for much more research, with a much broader base taking in more data gathered from a wider variety of locations, has become apparent.

One of the big problems that has worried many of us as landowners and as pulpwood users has been the terrific loss in our poplar stands because of the *Hypoxylon* canker. Very little is known about it, its prevalence, rate of spread, and, particularly, how it can be stopped. For a number of years several of us have talked to those we thought should be interested, the Forest Service, the Experiment Station, the forest schools, and the Departments of Conservation. Finally, in 1949 Dr. Ray Hansbrough, senior pathologist in charge of the New England Section of the Bureau of Plant Industry, was given the assignment of seeing what could be done. It is noteworthy that we had to go to New England for a pathologist. We have none in the Lake States attached to the Forest Service or to any of our state conservation departments. Dr. Hansbrough, being a very busy person with all of New England to cover, could spend only a month or so in the Lake States. Most of his time available for the Lake

States had to be devoted to studying the problem and getting the field procedure organized. He could do little of the field work personally. The funds allotted to him allowed him to hire one young forester as an assistant for the summer months. In order to speed up the work we at Northern Paper Mills assigned one of our foresters to help, which enabled us to get the data on twice the number of plots that would otherwise have been possible. Thus the work was started. The Government funds allocated for this work for 1950 were to be no larger than those for 1949, so that I got in touch with a few other mills, found that they were interested, and called for a meeting with Dr. Hansbrough to plan for the work in 1950. Representatives of five mills attended, and in a few moments Dr. Hansbrough was pledged all the assistance he could possibly use.

From this meeting came the suggestion that we combine and push research on other problems in the management of poplar lands. Calls for another meeting were sent out, and eleven mills responded. Again a little discussion quickly broadened the scope, this time to take in management problems of any or all other species rather than just poplar. The meeting was followed by another one with the staff of the Lake States Experiment Station. It was suggested that industry could supply the manpower to do the field work for many of these research problems; the work would be done on their own lands; industry would get the benefit of the training and increased interest of their own personnel. The Experiment Station would furnish the needed planning and correlation of the projects and publish the results.

The industry group suggested that the field was large enough to have the Station assign a full-time man to promote, organize, and correlate these industry projects. Being limited for the immediate present by their current budget, the Station was unable to do that. A program was set up for the year of 1950, however, and the following projects were planned for action: (1) continuance of the Hypoxylon canker study; (2) study of reproduction under various conditions in our spruce, balsam, and cedar swamps; and (3) discing to promote reproduction.

Early in March, 1951, another meeting was held in St. Paul to review the results of the previous year's activities. Dr. Hansbrough reported on the Hypoxylon study. A wealth of data was on hand, but only the major factors had been analyzed, owing to lack of

personnel. Much more remains to be done on the analysis alone. No definite solutions for the control of this disease were apparent, though there were noted two distinct trends in the incidence of it which may give us some leads. It was decided to continue the study by establishing permanent plots throughout the Lake States.

The companies offered to undertake the work of establishing such plots and to gather the necessary data. This is one of the projects on the program for the coming year (1951). The discing project will also be followed up and developed this year, as will the study of swamp reproduction. These projects seemed to be enough for the present.

Thus we have a good start on this research program. We have proved that a number of distinct advantages are gained by coöperative effort, such as the following:

1. The work of the Experiment Station can be enlarged and speeded up to a considerable extent. Timber-holding companies are glad to donate the time of their employees to work on any practical problem which is of interest to them. Many companies are interested in the same problem, so that this additional help can be very material.

2. By having their own men investigate these problems on their own land, companies can train them, keep them up to date, stimulate their interest. They see the results for themselves and do not have to try to dig them out of a mass of publications, which most of them are too busy to peruse.

3. Experiments will be carried on over much wider areas and scattered so as to cover a variety of conditions, and, therefore, results will be much sounder and more reliable than when based on limited areas in a limited region.

4. This expansion of research work can be done without the necessity of asking Congress for large increases in appropriations. I believe that on March 15 all of us agree that our government is spending too much, and doubtless wasting a large part of it, but on this type of research we get direct benefit from every dollar we spend, without a considerable portion of it being wasted in Washington before the balance is returned to us locally.

5. Research work already undertaken by the various forest schools, states, and their departments of conservation could and

should also be incorporated into this program so that the individual efforts may be added to the whole. Some of the work being done as individual efforts is now in duplication of that carried on by others, and much more progress can be achieved if all efforts are correlated. Parts of some of the problems undertaken would make excellent subjects of research for graduate students working for their master's or doctor's degrees.

Our experience has made it quite apparent that we do need two things:

1. A qualified pathologist stationed in the Lake States, presumably attached to the staff of the Experiment Station. We certainly have plenty of problems that require the services of such a man. I believe the Lake States Experiment Station is the only one in the whole country that does not have a pathologist on its staff.

2. Some one man who would have the responsibility of promoting this coöperative program to make it most effective. It will take considerable contact work in visiting various companies, becoming familiar with the problems they are individually interested in, ascertaining those which are common to several companies, and setting up the procedure so that the work can be done on a uniform basis and results can be analyzed. To do this personal contacts are needed. Correspondence cannot be effective.

It may be that one man can fill both of these needs; at least we feel strongly that these are jobs with high priorities. As a team with all pulling together we get results impossible to achieve by individual efforts.

NORTHERN PAPER MILLS
GREEN BAY, WISCONSIN

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